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Biodiversity of the African savanna woodlands: How does it change with land use?

Hemant Gangaprasad Tripathi

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School of GeoSciences

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Abstract

The savanna woodlands of Southern Africa, colloquially termed the miombo, are poorly described in terms of biodiversity compared to other biomes. They have therefore been underrepresented in the wider understanding of how land use intensification is shaping global biodiversity. Land use change is known to reduce biodiversity and disrupt intactness of ecological communities with consequences for ecosystem functioning, resilience, and services. Miombo woodlands are described as biodiversity hotspots due to a high endemism of species and the presence of megafauna. At the same time, they are also considered dynamic socio-ecological systems shaped by disturbances and the land use activities of people. The patterns of biodiversity change in these tropical ecosystems may, therefore, have their own unique contexts, understanding of which will be essential for biodiversity and land use management in these ecosystems.

In this thesis, I identified the patterns of biodiversity change in response to the two major land use practices in the two dominant woodland types in southern African woodlands: the selective logging due to charcoal production in the mopane woodlands, and agricultural expansion in the miombo. I also examined the impact of two main disturbance agents, humans and elephants, on habitat structure and biodiversity in mopane woodlands. Across all chapters in this thesis, I investigated the effects of land use change and habitat modification on biodiversity empirically using chronosequences. To understand biodiversity change, I employed a hierarchical multilevel modelling approach making inferences at the three levels of ecological communities: species, community, and meta-community (set of ecological communities at different sites).

I selected six villages in the charcoal production hotspot of southern Mozambique and carried out field surveys for three taxonomic groups: trees, mammals and ground beetles. I modelled the counts of trees and beetles and incidence of

mammals using meta-community occurrence models in a Bayesian framework with the intensity class of the villages, above-ground biomass and land cover type as predictors. The results suggested that the species richness of trees and mammals declined by 12 and 8.5 % respectively while that of beetles increased by 3.5%, albeit non-significantly. In addition, the beta diversity of trees decreased while that of mammals increased. The results show that while both trees and mammals reduced in richness, they responded differently to charcoal production in terms of community organisation. The trees underwent subtractive homogenisation (decrease in alpha and beta diversities) primarily because of deterministic processes induced by selective harvesting of tree stems for charcoal. Mammal communities, on the other hand, showed subtractive heterogenization (decrease in alpha, but increase in beta diversity) mainly due to random extinctions.

In the agriculture frontier of miombo-dominated northern Mozambique, I investigated the effects of fragmentation and habitat loss caused by agricultural expansion on diversity and composition of trees and mammals. I modelled the occurrences of trees and mammals using occupancy models with the fragmentation and quantity of woodland cover as predictors. The model showed that most tree species (n=10), mainly the timber and firewood species, linearly declined in population size as fragmentation increased. Mammals, on the other hand, showed a nonlinear response. Seven mammal species increased at the lower levels of fragmentation. However, at the higher levels, none of the mammal species increased while two declined. Similarly, the species richness of trees linearly declined, while that of mammals increased up to a fragmentation level of 55-65% and declined above this limit. The beta diversity of trees increased with fragmentation while that of mammals decreased. The results suggest that, although fragmentation reduces species richness of both trees and mammals, it affects their species compositions in different ways. Trees undergo subtractive heterogenization due to random species losses while mammals experience subtractive homogenisation mainly due to the combined effects of fragmentation-led habitat loss and intensified hunting.

Finally, this study concludes that, above 75% fragmentation or below 26% habitat quantity, both taxonomic groups endure biodiversity loss. The threshold results here corroborate similar habitat quantity thresholds (20-30%) observed elsewhere in different ecosystems. However, they differ with the widespread notion that above 30% habitat quantity, the effect of fragmentation is non-existent. The results here emphasize that taxonomic groups respond differently, the diversity and population size of mammals reduced only after the habitat threshold, whereas, those of trees showed linear decrease with fragmentation most likely due to fragmentation-led habitat loss.

Lastly, I examined the effects of disturbance by humans and elephants on habitat structure and bird diversity by conducting a space for time substitution comparison in the mopane woodlands of Zambia. To examine the woodland structure, I modelled the structural attributes of habitat (stem diameter, stand density, and basal area) using mixed models with the proportion of affected stems by humans and elephants as explanatory variables. I found that elephant disturbance was associated with higher stem diameters, low stand densities, but no change in basal area. Human disturbance, on the other hand, was related to reductions in stand density and basal area, but no change in the stem diameter. Further, I tested species and functional diversity of birds against the covariates of habitat structure and disturbance. I found that bird communities reduced in species richness in both, human as well as elephant disturbed areas. However, the functional diversity did not change with elephant disturbance. I concluded that human disturbance reduces woody biomass (basal area is correlated with woody biomass) of mopane woodlands and functional diversity of birds whilst elephants do not.

In this thesis, I conclude that human driven land use change in the miombo woodlands erodes alpha diversity of all taxonomic groups. However, increases in beta diversity of mammals with charcoal land use and trees in agricultural land use may maintain their diversities at the meta-community level.

Lay summary

The increasing human dominance across the globe has transformed the earth's surface. Human activities have altered the structure and reduced the amount of habitats. These habitat modifications have affected biodiversity by reducing the number and changing the composition of species. To reduce the rate of species loss, it is important to understand the patterns of biodiversity change. However, not all ecosystems are well-studied. Compared to the other ecosystems, the dry woodlands in southern Africa are poorly described in terms of biodiversity. The broad-leaved mesic woodlands locally termed miombo are a dominant vegetation type in southern Africa. Miombo supports unique and important biodiversity. The biodiversity of miombo is threatened due to the increasing human influence. Expansion of agriculture for crop products, and selective logging of large trees for making charcoal are the dominant human activities in these woodlands. In addition, the increasing human presence has pushed and restricted elephants to the few non-human and protected areas. In higher densities, elephants are known remove woody stems by pushing over and pollarding and, as a result, converting the woodland habitat to a more shrub dominated system. In this thesis, I investigated how these three major disturbances – agriculture expansion, charcoal production, and elephant-human disturbance, affect biodiversity in the miombo region. My study shows that these disturbances reduce the number of species, a common observation in many studies across the globe. However, my study also demonstrates that different taxonomic groups (birds, plants, mammals, and beetles) respond differently to disturbances and the loss of species richness is not the end of the road. In response to the selective logging for charcoal production, I found that mammals maintained biodiversity at the landscape-scale through dissimilarity in species compositions. In other words, although at a small-scale (500 m^2), the number of species did reduce, several such small-sites together in a landscape (e.g. 50 km^2) collectively maintained the total number of mammal species.

These small-sites together maintained the total biodiversity because they all had unique combinations of species. This pattern of reduction in species richness at the small-scale and increase in dissimilarity between small-sites is called (subtractive) heterogenization. However, this pattern was not uniform across all the species groups. For example, tree communities lost species at the small-scale and also at the large-scale. This pattern of species loss at both scales is termed (subtractive) homogenisation. These patterns also varied between the types of disturbances. While mammals underwent heterogenization in response to selective logging for charcoal production, they experienced homogenisation in response to agriculture expansion. Thus, my study highlights that the type of species group and land use activity should be taken in to account for effective conservation and land use management.

In case of elephant disturbance, there is a growing concern that elephants reduce woody biomass and diversity of species. Study here, however, underlines that the elephant disturbance in the mopane woodlands of Zambia does not reduce woody biomass and the functional diversity of birds.

Overall, the studies here point out that the biodiversity change is contextual, species groups and the land use in question should be taken into consideration before making any projections. The overall species richness may indeed reduce, however, it is not the end of the road, as land scape level biodiversity for some species groups may be maintained.

Declaration

I declare that the work described here is my own, except where indicated otherwise.

No part of this thesis has been submitted for any other degree or qualification.

Hemant Gangaprasad Tripathi

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Growing up in a tiny house in the bylanes of crowded Mumbai, little did I imagine that one day I will be writing my Ph.D. in one of the most beautiful cities in the world. It has been a great journey from there. On the way, I have met many people. Most of them have inspired and motivated me. Casey Ryan, my PhD supervisor, has had a strong impression. He introduced me to the savanna woodlands, encouraged me to think broadly, and inspired me towards statistics and ecology. He provided me enough freedom to explore and learn, and when I strolled off too far, he made sure to bring me back on track. He has been the best teacher I have ever come across. I dedicate all the good aspects of this thesis to him. My other supervisors, Kate Parr and Emily Woollen provided me guidance whenever I asked. Emily helped me during my first two field work seasons and made sure I don't goof up. Rose Pritchard, my PhD sibling, has been a great company. We started PhD at the same time and we handed-in together. During the course of this PhD, we have been on parallel sides of so many different things. From field-working simultaneously on either side of Zambezi to researching two parallel aspects of the savanna system – humans and animals.

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Contents

List of tables

List of figures

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 1
General introduction

Thesis outline

Compared to the tropical forests, the biodiversity of the savanna woodlands in southern Africa is poorly described. The understanding of how it changes with land use activities in these ecosystems is therefore limited. Identifying the patterns of biodiversity change in response to the dominant land use activities in the savanna woodlands of Mozambique and Zambia, therefore, became the key motivation for the work I undertook as part of this thesis. Here I describe this work. At the start of this thesis, I provide an overview of how land use is organising biodiversity across the globe, underline the potential research gaps and highlight the key patterns of biodiversity change. After this, I explain about the need for the savanna context in the global biodiversity-land use discourse. Then, I describe the biogeography and ecology of savannas in general and that of savanna woodlands of Africa in detail. I also provide a brief account of the social aspects of these woodlands. This sets the context for this work. I then discuss the dominant land use activities and summarise the existing literature on biodiversity response to land use in the savanna woodlands of southern Africa. This provides the background and underlines the motivation for this work. In the following sections of the introduction, I elucidate the research questions and hypotheses, general research approach, study area and key findings of this thesis. Then, in the subsequent chapters, I present the results of my research topics. These are:

1. Response of multiple taxonomic groups to selective logging due to charcoal production in the mopane woodlands of Mozambique (Chapter 2)
2. Mammal and tree community responses to agriculture expansion in the miombo woodlands of Mozambique (Chapter 3)

3. Effect of human and elephant disturbance on (a) habitat structure and (b) species and functional diversity of birds in the mopane woodlands across Zambia (Chapter 4).

In chapter 5, I summarize the results, discuss limitations and suggest areas of further research.

Biodiversity in a changing world

> 'It is interesting to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us.... Origin of Species (Darwin 1888)

The existence of life and its enormous diversity is the most remarkable feature of the planet Earth (Tilman, 2000; Mora *et al.*, 2011). The diverse array of organisms representing an intricate a web of life underpin the functioning of ecosystems, improve their stability and resilience, and provide essential ecosystem services (production of food, climate regulation, nutrient cycling, and cultural and crop pollination) on which human well-being depends upon (Schmid *et al.*, 2009; Hooper *et al.*, 2012). Historically, this web of life, has gone through a series of climate and environment-led gradual alterations such as speciation and extinctions, and abrupt shifts like mass extinctions (Raup *et al.*, 1982; Avise *et al.*, 1998; Celâl Sengör *et al.*, 2008; John Alroy, 2008; Blois *et al.*, 2010; Doughty *et al.*, 2013; Werdelin *et al.*, 2013). However, the modern (1500 CE) rates of species loss have been higher (~100 times; Ceballos et al. 2015, ~ 200 times; McCallum 2007) than the background rates of extinctions in the past. This is often described as a sixth mass extinction, mainly as a response to the increasing anthropogenic pressures on the planet (Pimm *et al.*, 1995; Barnosky *et al.*, 2011; Ellis, 2011; Dirzo *et al.*, 2014; Ceballos *et al.*, 2015, 2017). In addition to losing species with intrinsic values (Beckerman *et al.*, 1980; Gaston, 1998), this *biological annihilation* (Ceballos *et al.*, 2017) can lead to dramatic

simplifications in the complex web of life, impairing the functioning and resilience of ecosystems, with consequences on the well-being of people (Ehrlich *et al.*, 1983; Tilman, 2000; MEA, 2005; Hooper *et al.*, 2012; Tilman *et al.*, 2014; Hautier *et al.*, 2015; Isbell *et al.*, 2015). Thus, there is a growing interest in minimizing anthropogenic extinctions and maintaining the remaining biodiversity (Rands *et al.*, 2010; Berry *et al.*, 2016; Johnson *et al.*, 2017).

Table 1: Glossary with processes and concepts, and their explanation, and synonyms used throughout the thesis

Term	Definition
Community (or assemblages)	A group of organisms belonging to multiple species living in a specific space (Vellend, 2010)
Meta-community	A set of local communities linked by dispersal and source sink dynamics (Leibold *et al.*, 2004)
Source-sink dynamics	Spatial dynamics in which populations of species are maintained through migration from communities where growth rates are higher than the mean (*source*) to colonization in communities where growth rates have declined (*sink ;* Holt, 1985)
Community ecology	Study of patterns in diversity, abundance, and composition of species, and processes underlying these patterns (Vellend, 2010)
Species richness	Total number of unique species in a community (Vellend, 2010)
Species composition	A state of community determined by abundance or occurrence of species (Vellend, 2010)
Species diversity (or alpha diversity)	For the purpose of this thesis, species diversity corresponds to species richness of a sampling unit
Functional traits	Life history and ecological trait of species
Functional groups	Orthogonal groups composed of correlated functional traits (Swenson, 2014)
Functional diversity	Total volume of functional trait space (distance) occupied by all species in a community (Petchey *et al.*, 2002)
Beta-diversity	Pairwise average dissimilarity in species or functional group composition between communities (Baselga, 2010)
Dissimilarity	Compositional dissimilarity between pairs of sites (Baselga, 2010)
Turnover	Replacement of some species or functional groups in a community by others. Opposite of nestedness (Baselga, 2010; Melo *et al.*, 2014; J. B. . Socolar *et al.*, 2016)
Nestedness	When communities are nested subsets i.e. communities with lower species richness or functional diversity are subsets of communities with higher species richness or functional diversity. Opposite of turnover (Baselga, 2010; Melo *et al.*, 2014; J. Socolar *et al.*, 2016)
Land use	The human employment of the land (Meyer *et al.*, 1992)
Land cover	Physical and biotic character of the land surface (Meyer *et al.*, 1992)
Winners - losers	Winners = Species which persist or increase in population; Losers=species which become locally extinct

The increases in the mean global temperatures and frequency and intensity of climate extremes (climate change), and expansion and intensification of human activities and disturbances (land use change), mainly agriculture and logging, are the two major global change drivers (Aleman et al., 2016; Hansen et al., 2001; Oliver and Morecroft, 2014). The past periods of climate change in the earth's history, through extinctions, migrations, and adaptations, has shaped the modern biodiversity of the earth (Coope, 2004). Compared to the past climate change events and in response to the recent glacial to inter-glacial transition periods, relatively fewer species became extinct, while more species survived by developing tolerance and migrating to more suitable habitats (Coope, 2004; Jackson and Overpeck, 2010). The present and future climate change events, however, may be more rapid due to the rising CO2 levels in the increasingly human-modified earth as over 75% of the Earth's terrestrial surface is altered as a result of human land use (Blois et al., 2013; Hansen et al., 2001). Land use change resulting in deforestation, degradation, fragmentation, and modifications in quality and quantity of habitats will influence landscape structure (Lambin and Meyfroidt, 2011; Oliver and Morecroft, 2014; Zipkin et al., 2009). This will affect the movement of species, reduce their ability to shift their distributions in response to climate change, and decrease meta-community heterogeneity which underpins the natural resilience of ecological communities (Lalibert et al., 2010). Therefore, in the backdrop of land use change, the future climate change could be more detrimental to biodiversity (Blois et al., 2013; Oliver and Morecroft, 2014). However, ecological communities are known to be resilient and their response to climate change may not follow the predictions based on the models (Pimm et al., 2014; Willis and Bhagwat, 2009). Species response may be dependent on where the species are and the quality and quantity of habitats left by the land use change (Blois et al., 2013). Thus, since land use change influences and interacts with the effects of climate change on biodiversity, the understanding of how land use shapes biodiversity and habitats will be essential for projecting the possible consequences of future climate change on biodiversity.

Biodiversity, the variability in the manifestation of all life forms, also connotes the struggles to describe, quantify and conserve the diversity of life in a changing world (Gaston, 1998). Land use change is now considered a major driver of the ongoing biodiversity loss causing unprecedented declines in the number and composition of species (Newbold *et al.*, 2015) – the two fundamental expressions of biodiversity. In realisation of ongoing biodiversity crisis, international agreements such as the Convention on Biological Diversity (CBD) have attempted to impose restrictions and provide guidance to countries ratifying biodiversity reduction treaties. The target set in 2002 - "to achieve by 2010 a significant reduction of the current rate of biodiversity loss"(CBD, 2002) was not met (Rands *et al.*, 2010; Adenle, 2012). It was immediately followed by Aichi Biodiversity target for 2020 (CBD, 2010), which stressed upon reducing the loss of species and habitats and improving planning and sustainable management. Until now, the Aichi target has achieved mixed results (Tittensor *et al.*, 2014; Fenu *et al.*, 2015; Hagerman *et al.*, 2016). While, biodiversity awareness and datasets, area under protection and sustainable land management have relatively improved, the state of biodiversity has not (Tittensor *et al.*, 2014; Fenu *et al.*, 2015; Hagerman *et al.*, 2016). Biodiversity aspects of these targets however, are difficult to meet and monitor without a locally relevant framework for sustainable land use management. This is founded on a thorough understanding of the local patterns of biodiversity change, taking into account the associated thresholds of land use and tipping points of biodiversity (Rands *et al.*, 2010; Tittensor *et al.*, 2014; Gagné *et al.*, 2015; Hillebrand *et al.*, 2017). Thus, for conservation prioritization and more informed decision making, the understanding of drivers and consequences of biodiversity change is imperative.

In the global biodiversity-land use discourse, most studies show that land use change and intensification typically reduces biodiversity (Gibson *et al.*, 2011; Murphy *et al.*, 2014; Newbold *et al.*, 2015; Jung *et al.*, 2016; Betts *et al.*, 2017) and alters species composition (Nichols *et al.*, 2007; Clark *et al.*, 2012; Newbold *et al.*, 2016). However, the empirical knowledge about the patterns of biodiversity change is

restricted mainly to the community level average measures of diversity (Hillebrand *et al.*, 2017), few well-studied regions (Vellend *et al.*, 2017), and the endpoints of the land use and land cover change (McGill, 2015; McGill *et al.*, 2015). Even within the boundaries of these limitations, empirically observed trends of biodiversity have often been contradictory (McGill *et al.*, 2015). At the global level, studies consistently agree that biodiversity is reducing as the world is becoming more human-influenced (Barnosky *et al.*, 2011). However, at the smaller spatial scales (local scales), a number of studies through their contradictory findings underline the complex, idiosyncratic and contextual nature of biodiversity-land use relationship. In their global syntheses, Vellend et al. (2013) compared plant communities and Dornelas et al. (2014) examined multiple taxonomic groups (mammals, birds, fish, invertebrates, and plants), showing no systematic loss of alpha diversity. Supp & Ernest (2014) found identical results monitoring vertebrates and insect responses to experimental manipulations (eutrophication, logging, burning, and grazing). Likewise, in other studies, alpha diversity showed an increase or no significant change (Berry *et al.*, 2010; Edwards *et al.*, 2011, 2012).

Contradicting the above, Newbold et al. (2015) used 380 previous studies and performed a spatial comparison of multiple taxonomic group assemblages between undisturbed and human disturbed sites. They demonstrated the disruptive effect of land conversion on alpha diversities. Similarly, Murphy & Romanuk (2014) and several others (Gibson *et al.*, 2011; Burivalova *et al.*, 2014; Jung *et al.*, 2016) showed the negative effects of land use (land conversion or increases in land use intensity) at local scales.

These inconsistencies demonstrate that the response of biodiversity to land use may vary in three ways. First, diversity response differs between taxonomic groups (Burivalova *et al.*, 2014) and also on the basis of the biodiversity metric used (Kessler *et al.*, 2009; McGill *et al.*, 2015; Hillebrand *et al.*, 2017). This implies that to effectively assess the impact of land use on biodiversity, variability between different taxonomic groups and the multi-level hierarchical nature of ecological communities,

from individual species (population size) to communities (community size and composition) should be considered. Studies that took into account only community size - total species richness, and demonstrated no effect of land use, ignored the turnover component which could indicate resilience (local immigrations; Hillebrand et al. 2017) or resistance (invasions; Kennedy et al. 2002) capacity of the ecological communities.

Second, biodiversity-land use studies are geographically biased (Vellend *et al.*, 2013, 2017; Dornelas *et al.*, 2014) and may vary among habitats, regions and continents (Bongers *et al.*, 2009; Burivalova *et al.*, 2014; Phillips *et al.*, 2016), implying that the conclusions drawn from the global biodiversity-land use syntheses do not effectively represent the understudied ecosystems like that of the savanna woodlands of Southern Africa (Vellend *et al.*, 2013; Dornelas *et al.*, 2014; Murphy *et al.*, 2014; Supp *et al.*, 2014; Newbold *et al.*, 2015). More studies, therefore, are necessary in these ecosystems, especially as these are human managed semi-natural systems adapted to the land use activities of people and characterised by frequent disturbances (Stromgaard, 1985; Ryan *et al.*, 2011). The biodiversity in these socio-ecological systems may have different responses, being more resilient to intermediate land use changes (Kalaba *et al.*, 2013; McNicol *et al.*, 2015).

Third, intensity, type, and history of land use are known to influence biodiversity response (Davis, 2000; Ernst *et al.*, 2006; Slade *et al.*, 2011; Bicknell *et al.*, 2014; Burivalova *et al.*, 2014). Yet, many empirical studies (Vellend *et al.*, 2013; Newbold *et al.*, 2015; Jung *et al.*, 2016) have focussed on the endpoints of changes without taking in to account the starting points (grassland to croplands v/s forest to cropland; McGill 2015). In addition, in case of Dornelas et al. (2014) the inferences are based on the more intact sites (Cardinale 2014, but see Dornelas et al. 2014), ignoring the effect of past events, land use transitions and the related patterns of community organisation, possibly leading to bias.

Besides the above-mentioned caveats, biodiversity change is also scale dependent (Hamer *et al.*, 2000; Sax *et al.*, 2003; Tylianakis *et al.*, 2006), evident from the consensus about its decrease at global and disparities with the local scales. At the biogeographical scale, biodiversity change studies are less common (McGill *et al.*, 2015), and generally point towards regional scale extinctions often compensated by immigrations, mainly through non-native introductions by humans (Sax *et al.*, 2003). Biodiversity at the local scale, though most studied, is still the least understood (Sax *et al.*, 2003; McGill *et al.*, 2015). It is at the local scales where species frequently interact, affect ecosystem functioning and ecological processes, and influence the provisioning of ecosystem goods and services (Huston, 1999; Sax *et al.*, 2003; McGill *et al.*, 2015). The realisation of ecosystem services by people, and interventions by land use and most monitoring and management activities also operate at these small spatial scales ranging from 0.1 to 10 km^2 (Sax *et al.*, 2003; McGill *et al.*, 2015; Jung *et al.*, 2016).

To manage biodiversity for improving ecosystem functionality and ecosystem service provisioning, and identify thresholds and tipping points, we thus need to improve our understanding of biodiversity and biodiversity change at the local scales. In this thesis, I focus on how land use organises biodiversity in the understudied woodlands of southern Africa using multiple taxonomic groups at such local scales.

How does land use organise biodiversity?

Biodiversity organisation refers to patterns in the composition and diversity of species. It includes (a) changes in the total number of species (alpha diversity) and (b) variation in species compositions (beta diversity). Beta diversity further has two components: difference in composition due to turnover of species, and the difference in composition due to nestedness (Baselga, 2010; Socolar *et al.*, 2016). Nestedness is fundamentally a disintegration of the community through non-random ordered loss of sensitive species along environmental or ecological gradients (Baselga, 2010; Ulrich *et al.*, 2012). Following the framework described by Socolar *et al.*, (2016) the above-mentioned metrics of community structure can be classified into six types of patterns described in the table below.

Table 2: Patterns in community structure based on Socolar et al.*, (2016)*

	Alpha-diversity trend	Beta-diversity trend	Type of patterns	Biotic pattern
1	-	+	Subtractive heterogenization	heterogenization
2	+	+	Additive heterogenization	
3	-	–	Subtractive homogenization	homogenization
4	+	–	Additive homogenization	
5	-	no change	Subtraction	
6	+	no change	Addition	

Biodiversity organisation also refers to the individual species level dynamics where species undergo environment or habitat selection (also termed as ecological filtration; Püttker et al. 2015, or extinction filtration; Balmford 1995). This results in species *winners and losers* (McKinney *et al.*, 1999; Tabarelli *et al.*, 2012) which influence the community level patterns. The species *winners* are often the more disturbance tolerant species (or undesired species in case of selective logging), while species *losers* are the disturbance-sensitive species.

McKinney *et al.*, (1999) described the winner-loser replacement (WLR) phenomena, where few globally widespread disturbance-tolerant species replace many endemic disturbance-sensitive species leading to subtractive (loss of richness) biotic homogenisation (loss of beta diversity, see Table 2). In this thesis, WLR refers to the tolerant-sensitive replacement in local tropical communities as observed by Tabarelli *et al.*, (2012).

Organisation by land use refers to the different mechanisms by which land use activities (e.g. selective logging), and land use-mediated habitat modifications (alterations in quantity and quality of available habitat) structure communities. Understanding how land use modifies communities depends upon the identification of the underlying processes that explain the observed patterns in community assembly. A number of theories and models could be invoked to explain the above-mentioned community and individual-species level patterns (Vellend, 2010; Marquet *et al.*, 2014). To give an example, WLR leading to subtractive biotic homogenisation of mammals may happen when few *winners* - disturbance tolerant, generalist and widely-distributed species, replace many *losers* –sensitive, endemic or locally infrequent and specialist species. This can be explained through several niche models – resource competition, predator-prey and food-web (Tilman, 1986; Chase *et al.*, 2003), or meta-community deterministic models (Leibold *et al.*, 2004; Holyoak *et al.*, 2005). By contrast, WLR leading to subtractive biotic heterogenization which entails replacement of many ubiquitous *losers* by few non-ubiquitous *winners* can be explained by the stochastic neutral models (Hubbell, 2001). Vellend, (2010) synthesised the amassing number of theories and models into four fundamental classes of process – selection, drift, speciation, and dispersal. In the framework by Vellend, (2010), the above mentioned, WLR-biotic homogenisation can be explained by selection as the suitable species are selected over the other in response to a disturbance regime, and the WLR-heterogenization can be explained by drift and selection where species are selected (or filtered) randomly with equal probabilities.

Combining the synthesis of Vellend, (2010) with the spatial beta-diversity framework of (Socolar *et al.*, 2016) and observations by Segre *et al.*, (2014), I define six processes that may produce the community patterns I described above. I will use these patterns (Table 2) and the processes (Table 3) throughout the thesis to explain my observations. Also, the functional diversity patterns and processes will follow the same terms replacing species by functional groups, beta-diversity by functional beta diversity.

Table 3: Possible processes that may produce alpha-beta diversity patterns

	Type of patterns (Alpha/Beta)	Biotic pattern	Process
1	Subtractive heterogenization (-/+)	heterogenization	Stochastic extinction
2	Additive heterogenization (+/+)		Stochastic assembly + dispersal
3	Subtractive homogenization (-/-)	homogenization	Deterministic exclusion
4	Additive homogenization (+/-)		Deterministic assembly + dispersal
5	Subtraction (-)		Selection (filtering)
6	Addition (+)		Dispersal

The African savanna context to the global biodiversity change

There is a growing interest in understanding how land use is shaping global biodiversity at local scales, evident from the increasing number of global syntheses (Gibson *et al.*, 2011; Vellend *et al.*, 2013; Dornelas *et al.*, 2014; Newbold *et al.*, 2015, 2016, 2017). However, these studies lack geographical breadth (Vellend *et al.*, 2017) as they under represent one of the two dominant tropical biomes, the tropical grassy biome (savannas). Compared to the tropical forests, savanna ecosystems have received poor attention in the global ecology and conservation (Bond *et al.*, 2010; Murphy *et al.*, 2016) and inadequate representation in global biodiversity data sets (Newbold *et al.*, 2017). Nonetheless, they are biodiverse - although poorly documented - ecosystems containing unique sets of highly endemic flora and fauna (Bond *et al.*, 2010). Notwithstanding the obvious land use change and its potential to reduce biodiversity, the understanding of the trends of biodiversity-land use change in savannas, especially in the savanna woodlands of southern Africa, is rudimentary compared to the other tropical biomes. This is mainly because they have been consistently and widely misunderstood as artefacts of human disturbance, and thus, degraded ecosystems of low conservation value (Bond *et al.*, 2010; Murphy *et al.*, 2016).

Instead, most savannas are distinct ancient ecosystems (Bond *et al.*, 2008, 2010) shaped by frequent disturbances due to human activities and often herbivory (Langevelde *et al.*, 2003; Beerling *et al.*, 2006; Bond *et al.*, 2008; Ellis *et al.*, 2010; Archibald *et al.*, 2012). These disturbance regimes constantly cause alterations in the composition of ecological communities leading to establishment of disturbance tolerant (resilient) species, and removal of disturbance sensitive (extinction prone) species - 'extinction filtration' (Keddy, 1992; Balmford, 1995; Shaw *et al.*, 2002; Cianciaruso *et al.*, 2012).

Further, the intensity, frequency, and combination of disturbances vary over space and time imposing a diverse array of filters, organising communities differently across the landscape, resulting in higher beta diversity – dissimilarity between communities (Bond *et al.*, 2001; Orgeas *et al.*, 2001; Beck *et al.*, 2007). The prevalence of ecologically tolerant species along with the variability in composition makes the ecological communities in savannas more resilient to intermediate land use pressures compared to other tropical biomes. However, they may still undergo drastic declines beyond a certain threshold of land use intensity. The biodiversity change in context to these disturbance adapted ecosystems is therefore interesting and may provide new contexts to the global biodiversity-land use narrative.

In Southern Africa, the Caesalpinioideae woodlands – mopane and miombo – are the dominant savanna ecosystems and are considered one of the world's biodiversity hotspots. Like most savannas, the patterns of biodiversity change in response to land use in these woodlands is unevenly studied. In a recent synthesis, Newbold et al. (2017) focussed on tropical grasslands and savannas in Africa stating negative effects of land use on biodiversity. But their results had large uncertainties due to the patchy distribution of sites which represented only four of the 26 ecoregions in African tropical biomes. Their study, however, provides a much-needed framework by showing that the effects of land use on biodiversity in the African grasslands and savannas are larger than other biomes. Newbold et al. (2017) estimated that African tropical grasslands and savannas lost about 21.6% (95 % CI; 9.7 - 42.0) of species richness by 2005, 8% higher than the global average estimate 13.6% (9.1–17.8%) in Newbold et al. (2015).

Therefore, there is a scope for a better understanding of biodiversity and land use change in context to these understudied and underrepresented ecosystems: the savannas in general and savanna woodlands of southern Africa in particular. The context of these ecosystems will improve the global level understanding of how land use assembles biodiversity at local scales. The savanna woodlands are still relatively more intact compared to the other tropical biomes, but are anticipated to

be vulnerable to future land use changes (Aleman *et al.*, 2016). A thorough and timely understanding of the thresholds of land use-driven land scape processes (e.g. fragmentation and habitat quantity) and differences between land use types (selective logging v/s agriculture) will help make locally relevant and effective land use management and conservation policies.

The savanna ecosystems

Often described as grasslands with varying amounts of woody cover (Shorrocks, 2015), savannas are one of the dominant tropical biomes of the world occupying about 20 % of the land surface (Kottek *et al.*, 2006; Shorrocks, 2015) and 40% of the tropics (Solbrig *et al.*, 1996). Tropical temperature, distinct wet and dry seasons, unimodal low rainfall (~1000 mm, 3-7 months), and disturbances due to fire and herbivory are key determinants of savannas (Lehmann *et al.*, 2011, 2014; Staver *et al.*, 2011) that extensively occur in Africa, followed by South America, Australia, and India (Shorrocks, 2015). Savannas are, characteristically, distinguished from other ecosystems by the presence of two contrasting, competing and co-dominating life forms: the trees and C_4 grasses (Scholes *et al.*, 1997; Sankaran *et al.*, 2005). These life forms undergo complex competitive interactions, where one outcompetes the other reaching meta-stable states. The dynamics of tree-grass co-dominance, however, is complex and is determined by various factors from disturbance (fire and herbivory), to the niche separation (functional - root length) and phenological niche, to location (flooded savannas in south America; Solbrig *et al.*, 1996; Scholes *et al.*, 1997; Shorrocks, 2015). Depending on the dominance of grasses or trees, savannas can be subdivided into grasslands containing a continuous layer of grasses with widely scattered trees, or woodlands dominated by trees with a sparse understory of grasses (Scholes *et al.*, 1997).

The structure and productivity of savannas, conditional upon the regional species pool, influence its biodiversity (Solbrig *et al.*, 1996). In addition, fire and herbivory are the two major disturbing factors in savannas that alter its biodiversity directly

by causing mortality of individuals, and indirectly by modifying habitats (Staver *et al.*, 2009). On the basis of these factors, the biodiversity of savannas across the globe can be generalised to be mainly composed of: fire- and herbivory-adapted plants species, C_4 plant feeding animals (Shorrocks, 2015), presence of large mammals (relative to the local species pool) or high invertebrate biomass (Mistry, 2002; Radford *et al.*, 2014; Ferreira *et al.*, 2017) and low tree diversities (Mistry, 2002). In South America, the savannas have high plant species richness and very few savanna-specific faunal species such as pampas deer (*Ozotoceros bezoarticus*), the marsh deer (*Blastocerus dichotomus*) and the white-tailed deer (*Odocoileus virginianus*). In *Eucalyptus* dominated savannas of Australia, the faunal biomass is dominated by invertebrates (Andersen *et al.*, 1990, 2005). The large mammal species occur in low densities, mainly comprise of the introduced ungulates (Freeland, 1990), and in some regions the macropods such as the large red kangaroo (*Macropus rufus;* Kutt & Gordon 2012). The Indian savannas, similar to their African counterparts, typically consist of large grazers (*Rhinoceros unicornis* and *Elephas maximus indicus*) and big predators (*Panthera tigris tigris ;* Shorrocks 2015). The African savanna characteristically contain large mammals, high diversity of invertebrates and birds, and a large number of endemic plant species (Frost *et al.*, 1996; Mistry, 2002; Mittermeier *et al.*, 2003; Shorrocks, 2015).

In the following section, I describe the savanna woodlands of Africa, the focus of this study, in more detail.

The savanna woodlands of Africa

In Africa, savannas are the common vegetation type covering about 50% of the land area (Shorrocks, 2015). African savannas primarily consist of (i) Grass-shrub savannas, (ii) Tree-shrub savannas, (iii) Savanna woodlands, and (iv) Forest mosaics; representing a gradient of grass-tree dominance starting from the grassier to the more woody end of the spectrum (Shorrocks, 2015). Among the African savannas, while the deciduous woodlands are the most widespread savanna ecosystems, the broad-leaved mesic woodlands, characterised by the presence of non-nitrogen fixing trees of subfamily Caesalpinioideae, are the most dominant woodland types (Timberlake *et al.*, 2010). The Caesalpinioideae woodlands mainly occur in southern Africa and consist of two major types: miombo and mopane (Frost, 1996; Timberlake *et al.*, 2011). Miombo is a vernacular *Swahili* term for trees belonging to the Genus *Brachystegia* but is largely used to represent the savanna woodlands defined by the occurrence of tree species belonging to the closely related generas: *Brachystegia*, *Julbernardia* and *Isoberlinia* (Frost, 1996). Mopane, is a local term used to describe the woodlands dominated by *Colophospermum mopane*, often forming monospecific stands (Frost, 1996). Miombo is the most widespread, covering an area of about 2.57 million km^2, and is generally found in the nutrient-poor and well-drained soils. Whereas, the mopane, occupying about 0.4 million km^2, is the second most dominant woodland, mostly confined to the lower lying areas and the nutrient-rich soils (Frost, 1996; Timberlake *et al.*, 2010, 2011). The overall area of these southern Caesalpinioideae woodlands (3.6 million km^2) is collectively termed as the Miombo Ecoregion (Timberlake *et al.*, 2011). The Miombo Ecoregion (miombo region) can be considered as a biome consisting of the two dominant woodlands: miombo and mopane, along with the other open woodlands (e.g. Acacia, Combretum, Baikiaea, Burkea, and woodlands of mixed species; Timberlake & Chidumayo 2011; Byers 2001). The miombo region is the largest patch of deciduous tropical woodlands and dry forests in the world (Lawton, 1982; Campbell, 1996). It is bounded by the Angolan escarpment in the west, and the

beginning of coastal woodlands of Mozambique and Tanzania in the east. In the north, it is surrounded by the Congolian evergreen forests of the Congo basin and in the north east by the dry Acacia-Commiphora bushlands of Tanzania. In the south, it extends up to the grasslands and mixed Acacia woodlands of South Africa and in the south west up to the Acacia woodlands of Namibia and Botswana (Timberlake *et al.*, 2011).

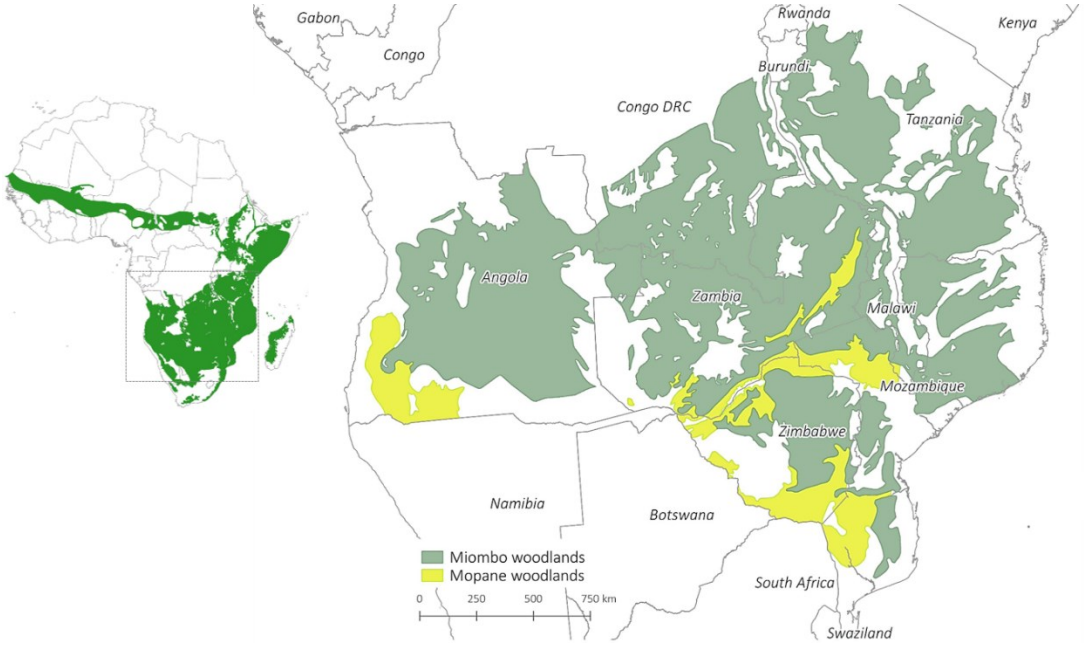

Figure 1: Map of potential extents of miombo region which consists of miombo and mopane woodlands with inset showing the savanna vegetation cover described by White (1983)

Figure 2: Miombo and mopane, the Caesalpinioideae woodlands, are the dominant vegetation type in the southern Africa. Both woodlands are impoverished in terms of canopy species. While, miombo is characterized by the presence of Brachystegia, Julbernardia and Isoberlinia, mopane often forms monospecific stands of Colophospermum mopane. Miombo occurs throughout the miombo ecoregion, while mopane woodlands commonly occur in the low lying areas and flood plain of major rivers in southern Africa – Zambezi, Luangwa, Limpopo and Kunene.

The boundaries of the miombo region overlap with the Zambezian Regional Centre of Endemism (White, 1983) indicating that it supports rich biodiversity and consists of a distinct set of species with a high degree of endemism (Frost, 1996; Timberlake *et al.*, 2011). The miombo woodlands are nutrient poor; due to which, at local scales they are impoverished in terms of alpha-diversity (Timberlake *et al.*, 2011). However, they still contain species of conservation importance (Mammals: Sable antelope and Lichtenstein's hartebeest; Birds: Miombo Grey Tit, Miombo Rock Thrush). Nonetheless, the biodiversity of the miombo region is maintained through the between-habitat diversity (Timberlake *et al.*, 2011). The miombo woodlands are intervened frequently by the non-miombo vegetation patches, the mopane, Combretum and Acacia woodlands, fire-induced tall grass savannas called Chipyas, spiny evergreen thickets associated with high termite mounds, riverine forests which occur near the banks of rivers, seasonally waterlogged treeless grasslands, Dambos, and other scattered patches of fire tolerant plants like *Pterocarpus angolensis, Burkea africana, Erythrophleum africanum*, etc. (Campbell, 1996). Also, between the naturally occurring miombo and non-miombo habitats, the region contains crop lands and fallows (Campbell, 1996). This heterogeneous assortment of fertile and non-fertile woodlands, fragmentation and reconnection of diverse habitats support rich floral and faunal assemblage and maintains biodiversity in the miombo (Byers, 2001; Timberlake *et al.*, 2011).

Miombo, being an important biodiversity region, is also equally significant for human well-being (Campbell, 1996). People living in Miombo largely depend on it for well-being and livelihood (Ryan *et al.*, 2016). Common Miombo species are mostly used for construction, weaving and energy production while non-miombo fruit producing species, tuber and bulbs of plants, leafy vegetables, mopane caterpillars, and animal meat are widely used as food (Ryan *et al.*, 2016). *Brachystegia* which is the dominating miombo plant species was used for making clothes during Mozambique war (Campbell, 1996). Oil from the kernels of Parinaria (*Parinari curatellifolia)* and *Marula (Sclerocarya birrea)* and jams from *Uapaca kirkiana* provide

food, energy and income generation (Mutanga, 2009). More than 50% protein need of the local communities is met through bush meat which involves animals ranging from small rodents to antelope (Campbell, 1996; Dewees *et al.*, 2011). In all, miombo region represents a complex socio ecological system that supports rich biodiversity and provides essential ecosystem services and supports livelihood and well-being of people.

Land use in the miombo ecoregion

Human presence in the miombo region dates back to the early Stone Age (Timberlake *et al.*, 2011). Hunting-gathering and shifting cultivation have been the dominant form of human land use, shaping the ecoregion, making it the social-woodlands of today (Timberlake *et al.*, 2011).

But, the densities of people in rural and urban areas has increased, therefore increasing their demand for agriculture and woodland products (Ellis *et al.*, 2010; Fisher, 2010; Rudel, 2013; UN, 2014). Agriculture expansion for subsistence and local markets (Rudel, 2013; Ryan *et al.*, 2014; Wallenfang *et al.*, 2015) is now a leading cause of deforestation in the sub-Saharan Africa. Similar to agriculture, the harvesting of wood fuel, is one of the common land use activities in southern Africa (Figure 2). Wood fuel and charcoal production, accounts for about 76% of total energy in the miombo region, with urban centres being the main consumers and drivers of the commercial charcoal production (Malimbwi *et al.*, 2010; Ryan *et al.*, 2016). Charcoal production in African context is commonly practiced by selective harvesting of large tree stems (Chidumayo *et al.*, 2013). Hence, it results in the loss of woody biomass and degradation of the woodland (Chidumayo *et al.*, 2013; Woollen *et al.*, 2016). Thus, small-scale agriculture and charcoal production are the dominant land use activities and major drivers of deforestation and degradation respectively in the miombo region (Chidumayo *et al.*, 2013; Ryan *et al.*, 2014). Other than humans, large herbivores, especially elephants, are one of the main determinants of the woodland structure in savannas of Africa. In the mopane region, the mopane

woodlands are the primary food source of elephants (Ben-Shahar, 1996; Styles *et al.*, 2000; Mograbi *et al.*, 2017).

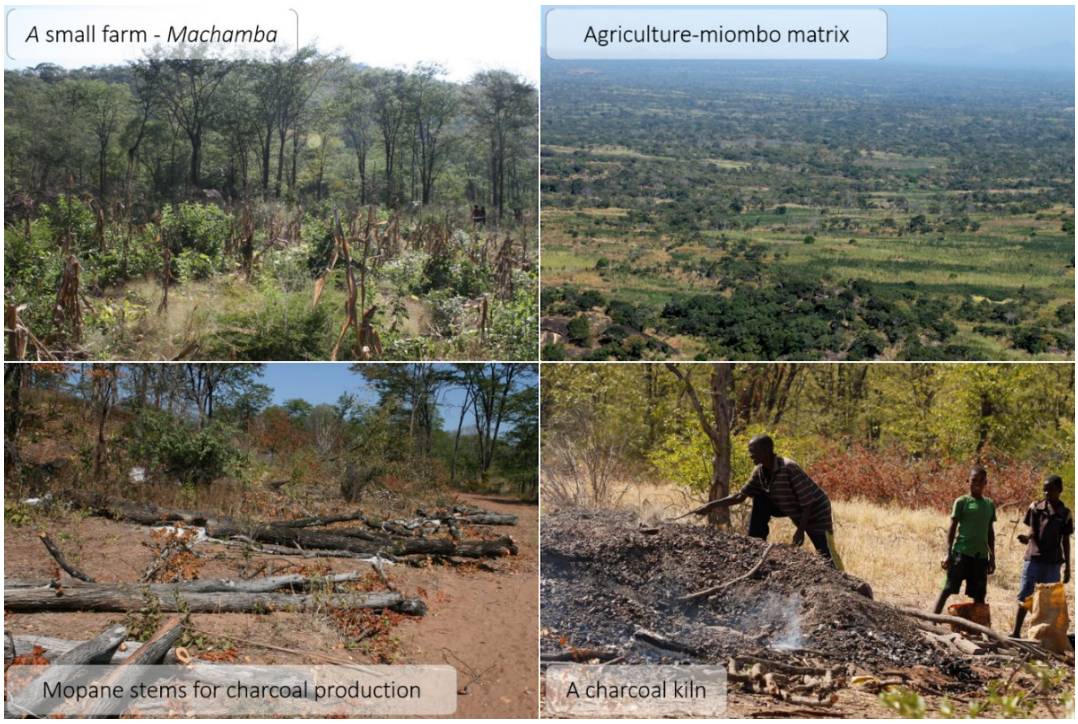

Figure 3: Expansion of small-scale farming to meet the needs of the growing rural population is main driver of deforestation in the miombo woodlands. As agriculture expands, the historical semi-natural, socio-ecological and heterogeneous agriculture-miombo matrix is more likely to become more agriculture dominated, human influenced, and simplified production oriented system. Charcoal is the most commonly used wood fuel in Africa primarily for household cooking. The commercial charcoal production, largely driven by urban demand, results in loss of woody biomass through selective logging of stems, preferably mopane. Charcoal is produced through carbonization of biomass through pyrolysis of stems in kilns.

Deforestation due to shifting agriculture is reducing the quantity of woodland habitats (Ryan *et al.*, 2014), and has pushed elephant populations to protected areas, thus concentrating and locally intensifying their impact (Cumming *et al.*, 1997). Elephants, being bulk feeders, browse, debark and pollard mopane stems and thereby alter the structure of the woodlands (Styles *et al.*, 2000; Kohi *et al.*, 2011). In higher densities, however, they can suppress biomass production and cause long term changes in the woodland condition (Ben-Shahar, 1996). In the savanna woodlands, the human land use, and elephant disturbance, which has been aggravated due to human land use, are therefore the leading causes of woodland modification.

Biodiversity-land use studies in the miombo

Knowledge about how biodiversity responds to land use in the miombo region is limited. Most studies are restricted to tree communities (e.g. Giliba et al. 2011; Shackleton 2000; Kalaba et al. 2013; Banda et al. 2006). Of the studies conducted in miombo region, Jew et al. (2015) demonstrate the negative effect of miombo woodland utilisation on butterfly communities. Elsewhere in Africa, in other dry woodlands, Ndegwa et al. (2016) and Kiruki et al. (2017) showed losses in density and diversity of tree communities in response to charcoal production, while Fontodji et al. (2011) noted the overexploitation of charcoal tree species, and showed reduction in soil faunal diversity. On the basis of fragmentation studies elsewhere (Dunning *et al.*, 1992; Andrén, 1994; Pardini *et al.*, 2010; Eycott *et al.*, 2011; Tscharntke *et al.*, 2012; Magrach *et al.*, 2014; Magioli *et al.*, 2015), agriculture land use in the miombo region at intermediate levels may be associated with higher land cover heterogeneity leading to increase in the landscape-wide species pool. However, when agricultural land cover expands, the quantity and size of woodland patches reduce disrupting the size and intactness of ecological communities (Bogaert *et al.*, 2011; Hanski, 2015).

The effect of charcoal production can be similar to selective logging. The selective logging - biodiversity studies across the globe commonly show reductions in alpha and beta diversities across multiple groups (Ernst *et al.*, 2006; Gibson *et al.*, 2011; Burivalova *et al.*, 2014). But a number of studies also show inconsistent results which differ on the basis of taxonomic groups (Burivalova *et al.*, 2014), habitats (Bongers *et al.*, 2009; Burivalova *et al.*, 2014), intensity, type and history of logging (Davis, 2000; Ernst *et al.*, 2006; Slade *et al.*, 2011; Bicknell *et al.*, 2014; Burivalova *et al.*, 2014), with some showing increase while others demonstrating no change in diversity (Berry *et al.*, 2010; Edwards *et al.*, 2011, 2012, 2014).

The effect of disturbance by elephants is relatively well studied, but also indicate inconsistencies. Cumming et al. (1997) showed that species richness of birds and ants decline in elephant disturbed areas, while Herremans (1995) noted no change in richness but alteration in composition of bird species. Further, Guldemond et al. (2017), in their synthesis across Africa, state that elephant disturbance does not affect diversity or composition of trees or vertebrate species. Botes et al. (2006) comparing dung beetle assemblages in sand forests of Mozambique demonstrated changes in species composition. Botes et al. (2006) also compared elephant and human effects and showed reduction in number of species with human disturbance.

Thus, the effect of land use or habitat disturbances on biodiversity in miombo region is poorly studied and is restricted to single taxonomic groups, mostly trees. And, no study has compared human and elephant disturbance in context to the miombo or mopane woodlands or have taken in to account changes in functional diversity.

Objectives, questions and hypothesis

The previous sections of this introduction highlight that the global understanding of how land use activities shape biodiversity at local scales lacks geographical breadth. The woodlands of southern Africa, dominant savanna ecosystems in the southern hemisphere, are largely underrepresented in the global biodiversity-land use discourses. Thus, exploring the patterns of land use-mediated biodiversity change in context to the savanna woodlands of southern Africa is the main objective of this thesis.

Biodiversity change is multi-faceted (Fukami, 2004; Hillebrand *et al.*, 2017). Separating multi-facet biodiversity responses: individual species, species richness, turnover and nestedness can help understand patterns of community assembly more effectively (Kessler *et al.*, 2009; Hillebrand *et al.*, 2017).

Also, species' responses to land use pressures vary between major taxonomic groups (Hilton-taylor *et al.*, 2009). So, understanding the patterns of community assembly using multiple taxonomic groups was another objective.

Charcoal production in the mopane woodlands and agricultural expansion in the miombo are the major land use activities in southern Africa. Their impacts on biodiversity is poorly described in context of these woodlands. These land use activities modify the structure and distribution of the woodland habitats. As of a result of habitat modifications, they alter the structure of ecological communities. To infer about the process and patterns of community assembly, I explored the species and community level responses to the intensity of charcoal production (chapter 2) and degree of fragmentation and habitat loss caused by agriculture expansion (chapter 3).

Further, in protected areas, elephant disturbance is known to affect the structure of the woodlands and alter its biodiversity (Harvey, 1997; Botes *et al.*, 2006). However, no study has tested if human and elephant disturbances in the savanna woodlands modify habitat and biodiversity differently. To explore how human and elephant disturbances structure habitats and organise biodiversity, I investigated relationships between intensity of disturbances, habitat attributes and species and functional diversity of bird communities (chapter 4).

The specific questions I investigated are:

Q1. How does diversity and composition of tree, mammal and ground beetle communities respond to charcoal production in the mopane woodlands?

Q2. How does fragmentation and loss of habitat due to agricultural expansion in the miombo woodlands affect tree and mammal communities?

Q3. How does human and elephant disturbance modify habitat structure and alter bird communities in the mopane woodlands?

The hypotheses corresponding to these questions are:

H1-Q1: Charcoal production most often involves selective harvesting of trees of the preferred size and species (Hosier, 1993; Chidumayo *et al.*, 2013; Woollen *et al.*, 2016). However, with increasing intensity of production (i.e. time since it started and amount of depletion it caused), the density of preferred individuals of tree species reduce (Arnold *et al.*, 2003). After depletion of the preferred species, charcoal production becomes relatively non-selective and involves harvesting of other available species in the region (Hosier, 1993). Also, people harvest other tree species for other purposes (e.g. firewood, woody construction; Woollen et al. 2016). Since the tree species are harvested selectively for charcoal or timber, I expect that charcoal production and related pressures will impose deterministic exclusion process on tree communities. This will result in more *species losers than winners,* with most *losers* being charcoal and timber-fire wood species. As a consequence, tree communities will experience subtractive homogenisation – reduction in alpha and beta diversity.

As charcoal production primarily filters out trees based on size, it causes reduction in the woody biomass (Woollen *et al.*, 2016). The loss of woody biomass reduces the quantity of resources (forage and habitat) for mammals (Kos *et al.*, 2012). As a result of resource depletion mammals may undergo competitive exclusions. This reduces community size and may increases the variability between communities if the competition pressures are stochastic (Segre *et al.*, 2014). For ground beetles, I expect charcoal production to cause species turnover without any significant loss of alpha diversity. The global synthesis by Nichols et al. (2007) showed that selective logging did not reduce the alpha and beta diversity of ground beetles. They further demonstrated that secondary forests, however, were associated with decline in alpha and increase in beta diversities. In high intensity charcoal production, with reduction in woody biomass, the mopane woodlands transform to low biomass system dominated by the shrub-form of mopane with increased grass cover. This transformation in micro-habitat structure – opening of canopy, change in

understory, may result in turnover in ground beetle communities as species with preference for woodlands will decline and species preferring ground vegetation will increase in relative dominance.

H2-Q2: Agricultural expansion is associated with increasing fragmentation and reduction in quantity of woodland habitat (Wade *et al.*, 2003; Bogaert *et al.*, 2011). Fragmentation intensifies edge effects as it opens up more woodlands patches (Broadbent *et al.*, 2008). On the edges, the most commonly occurring tree species are more likely to undergo decline in densities due to over harvesting. As the woodland patches shrink and become more fragmented, the originally dominant tree species are replaced by the few originally rare and disturbance-tolerant tree species. This results in loss of species richness and turnover in species composition. Thus, I expect, agricultural expansion will reduce species richness and increase beta diversity (subtractive heterogenization) in tree communities.

Mammals not only experience increased predation on the edges, but also competitive exclusion due to contraction of habitats (Santos-Filho *et al.*, 2012). At intermediate levels of fragmentation, when the woodland patches are relatively closer in distance, mammal species explore multiple habitats avoiding competition and thereby increase in diversity. However, as habitats shrink and become more isolated, woodland-preferring species decline, while species that can utilise the agricultural areas survive. Thus, I expect fragmentation to have non-linear effect on mammals and result in subtractive homogenisation at higher levels of fragmentation.

H3-Q3: Humans and elephants both utilise the mopane woodlands. Humans selectively harvest all the stems that match their criteria. Elephants, on the other hand, browse on trees below a certain size (<4 m height) threshold (Smallie *et al.*, 2000). In addition, elephants prefer revisiting previously utilized and coppiced stems (Smallie *et al.*, 2000). Based on this prior knowledge, I expect that humans and elephants will affect different attributes of the habitat and will be associated with

different structural forms of mopane woodlands. Following their dissimilar effects on habitat attributes, I expect they will affect species and functional diversity of birds differently.

General research approach

To answer the above research questions, I used space-for-time substitution, field data and remote sensing, and statistical modelling, all combined with literature review for inference. To collect occurrence data for multiple species I employed different survey techniques. I used belt transects (Q1) and camera traps (Q2) for mammals, circular vegetation plots for trees (Q1, Q2 & Q3), pit fall traps for ground beetles (Q1), and point sampling for birds (Q3).

To investigate effects of charcoal production, I selected 6 villages representing a gradient of charcoal production intensity from low to high based on time since the start and peak of charcoal production. I also accounted for effects due to land cover and biomass. I investigated the effects of fragmentation and habitat quantity by using the degree of fragmentation (Land Division Index), proportion of woodland cover lost between 2007 and 2014, and quantity of woodland cover present in 2014 as predictors. For the effect of human and elephant disturbance, I used the proportion of stems affected as an indicator of intensity. I classified disturbance as human when stems had sharp cuts and elephant where affected stems showed signs of debarking and pollarding.

For Q1 & Q2, I analysed the multi-species occurrence using hierarchical meta-community models (Dorazio *et al.*, 2005) in a Bayesian framework using Markov Chain Monte Carlo (MCMC) simulation. For Q3, I first used hierarchical clustering to identity the structural forms of the mopane woodland. Then, I used tree regression models to test the association between structural forms and disturbances. Further, to examine how disturbances affect habitat attributes and diversity of birds, I constructed statistical models and selected the best model by backward selection.

For Q3, as the plots were clustered within 1 km² grids, I used mixed effects models. Across all questions, I examined individual species and community level responses.

Study areas

All questions focus on savanna woodlands in southern Africa. Q1 and Q2 focus on Mozambique, while Q3 on Mopane woodlands of Zambia (Figure 3). Q1, the charcoal production chapter is based in the Gaza province of Mozambique, a charcoal production hotspot of the country. The agricultural expansion chapter (Q2) represents the agriculture land use dominated miombo landscape in the Gurué district of northern Mozambique. The human-elephant impact chapter (Q3) covers the mopane woodlands in Zambia which occur in the eastern part of the country.

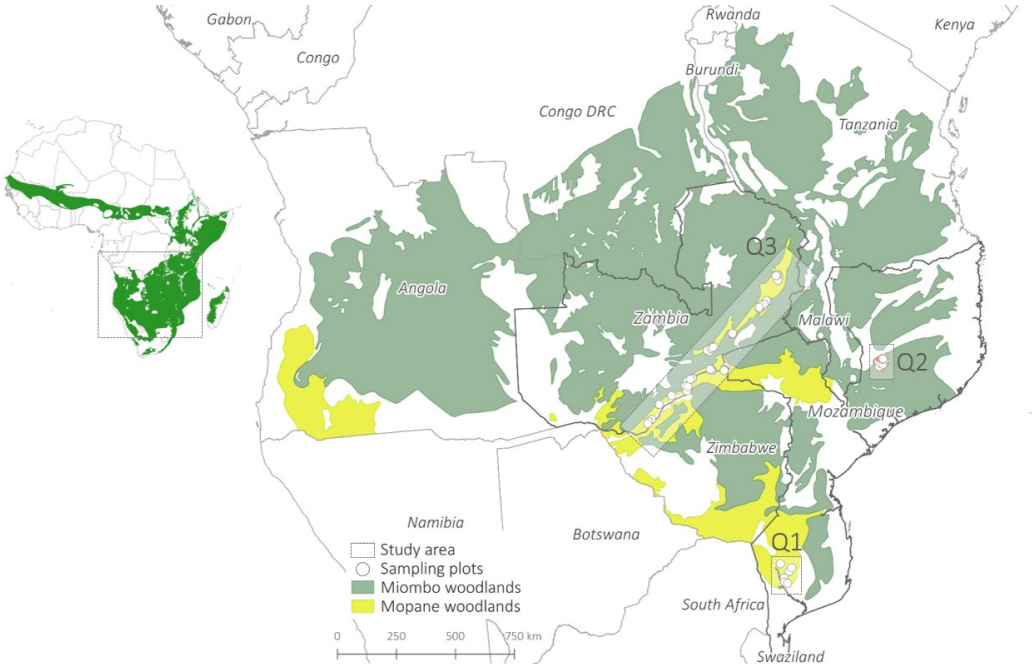

Figure 4: Map of potential extents of miombo and mopane woodland based on Ryan et al. (2016)*, with sampling plots and study areas for research questions (Q1, Q2 and Q3) described above overlaid. While Q1 and Q2 focused on one area, Q3 covered the entire mopane woodland in Zambia. The inset shows the savanna vegetation cover described by* White (1983).

Key findings of this thesis

The main results of this thesis are:

Land use intensification in savanna woodlands reduces diversity and alters the composition of ecological communities. The two dominant land use activities (charcoal production and agriculture) and disturbances (human and elephant) were associated with reductions in species richness and shifts in composition of trees, mammals and bird communities. However, ground beetle assemblages did not respond significantly.

The land use activities impose dissimilar selection processes on communities. Charcoal production imposes deterministic exclusion on trees resulting in loss of species and biotic homogenisation of tree communities. Mammal communities, however, undergo stochastic competitive extinctions resulting in reduction in alpha and increase in beta diversity.

Agriculture expansion, through increase in fragmentation and loss of woodland habitats, imposes edge and habitat loss effects. Fragmentation intensifies harvesting on the edges of woodland patches reducing the number of tree species. However, tree species are lost primarily due to conversion of woodland patches in to small-farms. The clear felling of trees facilitates random removal of tree species resulting in replacement of dominant species by the infrequent secondary vegetation tree species. The persistence of species which were earlier non-ubiquitous causes the tree communities to undergo drift in composition. In other words, increase in beta-diversity or biotic heterogenization. Biotic heterogenization may indicate existence of stochastic exclusion processes on tree communities. Mammal communities on the other hand show non-linear and deterministic response to agriculture expansion. They increase in diversity and likelihood of occurrence at the intermediate levels of fragmentation, and reduce when fragmentation is above 75 % or habitat quantity is below 26%.

Response to land use varies between taxonomic groups: The three taxonomic groups I investigated in the charcoal production hotspot responded in different ways. Also, in the agriculture expansion frontier, mammal and tree communities assembled differently. Many studies show that fragmentation affects biodiversity after the habitat quantity reduces below ~30%. Here, we show, this may not be true for all taxonomic groups. Tree communities in Q2 showed a linear decline with fragmentation, whereas mammals started to decline only at the higher levels of fragmentation (~75%) when habitat quantity fell below 26%.

Human and elephant disturbances are associated with different structural forms of the mopane woodlands. Human and elephant disturbance, both, reduced stand density. However, mean stem size (DBH) significantly increased with elephant disturbance. This maintained the total basal area (correlated to biomass) of the elephant disturbed woodland. In contrast, basal area significantly reduced with human disturbance. Therefore, in elephant disturbed areas, mopane woodlands have lowest stand density, but higher stem size, while human affected plots have reduced stand density and basal area.

Human and elephant disturbances both reduce species diversity of birds, but affect species compositions and functional diversity differently. Elephant disturbance was associated with reduction in beta diversity of bird communities without any significant reduction in functional diversity. Human disturbance, on the other hand, was associated with reduction in functional diversity without any significant effect on beta diversity of birds. This means that bird communities in elephant disturbed areas undergo biotic homogenisation without functional convergence, while in human disturbed areas, they undergo functional convergence without biotic homogenisation.

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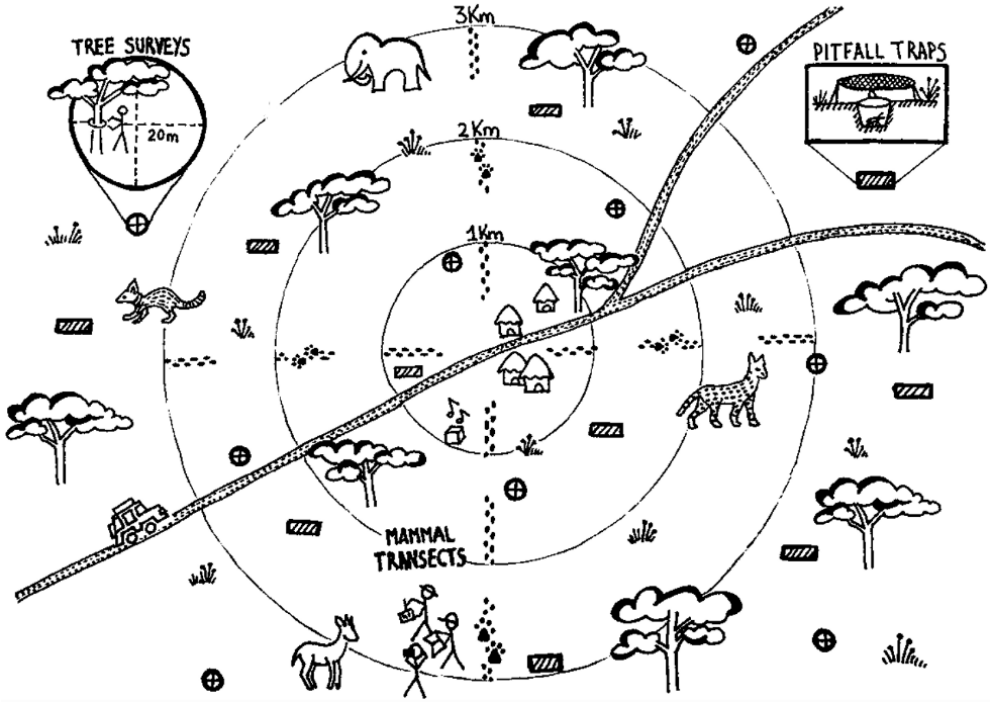
Chapter 2

How does biodiversity respond to charcoal production in the mopane woodlands?

Hemant G. Tripathi, Casey M. Ryan, Emily S. Woollen



HGT conceived the research questions with inputs from CMR. HGT developed the study design with help from CMR. HGT collected the mammal and ground beetle data. ESW collected the tree data and made the supervised land cover map. CMR prepared the biomass map. HGT collated and analysed the data, and wrote the manuscript. CMR provided suggestions for analysis and comments on the manuscript.

Abstract

Aim: The African savanna woodlands are dominant and biodiversity important ecosystems in the southern hemisphere. Yet, they are underrepresented in the global land use-biodiversity discourse. Selective logging for charcoal production is a dominant land use activity in southern Africa. The mopane woodlands are preferentially used for charcoal production to extract a better quality charcoal. The aim of this study was to understand how selective logging for charcoal production structures communities of multiple taxonomic groups.

Location: Mopane woodlands in the Gaza district of Mozambique.

Methods: In this study, we used a single-season comparison of chronosequence which represented a gradient of charcoal production intensity. We sampled trees, mammal and ground beetles and examined their individual species-level and community-level responses to intensity, land cover, and woody biomass. We used multiple measures of community-level response: species richness, turnover, and nestedness. We employed single-season meta-community occurrence models to estimate the species and community-level parameters. These models were analysed using the Bayesian framework.

Results: In response to the charcoal production intensity, the occurrence of trees and mammals reduced by 34.5 % and 21.5 % respectively, while that of ground beetles did not significantly change. Trees and mammals showed the *more losers than winners* phenomenon. Species richness of trees and mammals declined at the rate of 12% and 8.5%, respectively, with each increasing level of intensity (1 to 6). With intensity, the turnover component of beta-diversity of trees decreased by 12%, whereas, that of mammals increased by 98%. In addition, the nestedness of tree communities increased (85 %), while that of mammals decreased (-15.5%). The species richness or beta-diversity of ground beetles did not significantly vary with intensity.

Main conclusions: Charcoal production reduced species richness and altered species composition of two of the three taxonomic groups we studied. It had dissimilar effects on taxonomic groups. Charcoal production was associated with subtractive homogenisation (loss of alpha and beta diversity) of trees and subtractive heterogenization (loss of alpha, but gain in beta diversity) of mammals. These patterns indicate that charcoal production may be structuring communities through different processes – deterministic exclusion for trees, stochastic extinction for mammals and no effect on beetles.

Keywords: Africa, mopane woodland, savanna, selective-logging, charcoal production, taxonomic groups, trees, mammals, ground beetles, alpha-diversity, beta-diversity, occupancy, Bayesian, Mozambique.

Introduction

Land use change alters biodiversity (Newbold *et al.*, 2015), with global implications for ecosystem structure and function (Cardinale *et al.*, 2012; Hooper *et al.*, 2012), and impacts on human wellbeing (MEA, 2005a; TEEB, 2010). In southern Africa, charcoal provides about one third of primary energy and its production is a major land use activity (Chidumayo *et al.*, 2013). However, the impact of charcoal production on biodiversity is not well studied. Here we present a chronosequence study of the impact of charcoal production on the diversity and composition of three taxonomic groups: trees, mammals and ground beetles.

Charcoal production is one of the main drivers of disturbance in the mopane woodlands (Malimbwi *et al.*, 2010; Chidumayo *et al.*, 2013; Woollen *et al.*, 2016), one of the dominant savanna ecosystems in southern Africa (Makhado *et al.*, 2014). As charcoal production primarily involves selective harvesting of large trees — preferably of *Colophospermum mopane* in the mopane woodlands or of other high wood-density species in related systems (Chidumayo *et al.*, 2013; Philomena Kumapley *et al.*, 2016; Woollen *et al.*, 2016) — it leads to loss of woody biomass (Chidumayo *et al.*, 2013) and depletion of the preferred species (Arnold *et al.*, 2003).

This modification of structure and composition has cascading effects on ecological communities (Ndegwa *et al.*, 2016; Kiruki *et al.*, 2017). It imposes new environmental filters that may restructure communities of different taxonomic groups in different ways as observed in the recent selective logging-biodiversity syntheses (Gibson *et al.*, 2011; Burivalova *et al.*, 2014). The changing biodiversity will have consequences on availability and resilience of ecosystem services on which local human communities depend (Scholes *et al.*, 2004; Ryan *et al.*, 2016; Woollen *et al.*, 2016). To clearly understand the consequences of charcoal production on biodiversity and biodiversity-driven ecosystem services, it is important to know the direction and pattern of biodiversity change, i.e. restructuring of communities with-in and between various taxonomic groups.

Knowledge about how biodiversity responds to charcoal production is restricted mainly to impact on tree communities, and there have been no studies in mopane woodlands. In the floristically-related miombo woodlands, Jew et al. (2015) demonstrated the negative effect of tree harvesting on butterfly communities. In other dry African woodlands, Ndegwa et al. (2016) in Mutomo and Kiruki et al. (2017) in Kitui (both in Kenya) have shown losses in density and diversity of tree communities in response to charcoal production. Fontodji et al. (2011) in Togo also noted a correlation between the overexploitation of charcoal tree species and reduction in soil faunal diversity.

Selective logging, which has been better studied for timber extraction, is likely to have a similar impact on biodiversity to that of charcoal production. The selective logging-biodiversity investigations point towards negative effects (loss of alpha as well as beta diversity) across multiple taxonomic groups (Ernst *et al.*, 2006; Gibson *et al.*, 2011; Burivalova *et al.*, 2014). However, a number of studies also underline the idiosyncratic and contextual nature of biodiversity-selective logging or harvesting relationships. They demonstrate that biodiversity response varies between taxonomic groups (Burivalova *et al.*, 2014), habitats (Bongers *et al.*, 2009; Burivalova *et al.*, 2014), intensity, type and history of logging (Davis, 2000; Ernst *et al.*, 2006;

Slade *et al.*, 2011; Bicknell *et al.*, 2014; Burivalova *et al.*, 2014), and may increase or show no change (Berry *et al.*, 2010; Edwards *et al.*, 2011, 2012, 2014).

Charcoal production presents a unique case as it is selective on the basis of size (>30 cm DBH; Chidumayo 1993) and wood density (high density spp. make longer burning charcoal) and thus preferred tree species (Hosier, 1993; Chidumayo *et al.*, 2013). Charcoal production is highly selective at the initial stages of production (Woollen *et al.*, 2016). However, as the intensity of production (i.e. time since it started and amount of depletion it caused) increases and the density of large stems of preferred species decrease (Arnold *et al.*, 2003), harvesting for charcoal moves to other available species (Hosier, 1993). At different intensities, charcoal production may therefore structure the ecological assemblages in different ways. Tree communities at low intensities of charcoal production may not show a drastic decrease in diversity, as only few individual species are affected (Kiruki *et al.*, 2017). However, at higher intensities they may undergo decline in population size of a majority of species(mainly tree species that are utilized for charcoal production, construction and firewood) (Woollen *et al.*, 2016), resulting in a decline of species richness. Also, as many desired tree species are preferentially targeted, the woodlands are left with the few, locally wide-spread, but less desired, secondary growth- and disturbance-tolerant tree species (Kalema *et al.*, 2012; Kiruki *et al.*, 2017). As a consequence, the tree communities undergo the '*few winners many losers*' paradigm (McKinney *et al.*, 1999; Tabarelli *et al.*, 2012).

As charcoal production primarily filters out trees based on size, it causes reduction in the woody biomass (Woollen *et al.*, 2016). The mopane woodlands are important sources of food and habitat for faunal diversity (Styles *et al.*, 1997; Hooimeijer *et al.*, 2005; Kos *et al.*, 2012). With reduction in woody biomass in the mopane-dominated landscape, the quantity of habitat and forage for mammals shrinks. This may push mammal communities to competitive exclusions resulting in reduction in number of species as demonstrated by Burivalova *et al.*, (2014) in their global synthesis comparing effect of logging intensities on tropical biodiversity. Smaller organisms

such as ground beetles may experience different community structuring processes. In their global synthesis, Nichols et al. (2007) showed that selective logging did not reduce the alpha and beta diversity of ground beetles, though alpha and beta diversity of ground beetles were both lower in secondary vegetation. Selectively logged forests retain high degree of forest cover and therefore do not drastically alter the habitat and resources that structure ground beetle communities (Nichols *et al.*, 2007). However, in case of the selective logging for charcoal production, as we discussed above, logging is selective at the initial stages, becomes non-selective and depletes woody biomass with increase in demand for charcoal. The loss of woody biomass results in a low-biomass shrub-dominated habitat with more grass cover. This may cause habitat filtering of open canopy- and grass habitat-preferring ground beetle species, and a concomitant loss of woodland preferring species (Vance *et al.*, 2003). Hence, with increasing intensity of charcoal production, ground beetle communities may undergo turnover in species composition. The impact of charcoal production on biodiversity may be further amplified and compounded when coupled with other human induced disturbance such as cattle grazing, hunting and burning (Hosier, 1993).

We conducted the present study with the objectives of understanding the impact of charcoal production on biodiversity in mopane woodlands and exploring new contexts in the land use-biodiversity relationship. Since biodiversity responses can be multi-faceted and vary between taxonomic groups, we examined biodiversity using three taxonomic groups (trees, mammals, and ground beetles) at multiple levels (community and individual species) and using multiple metrics (alpha and beta diversity, turnover and nestedness of beta-diversity). We present here a multi-species assemblage-level assessment of biodiversity response to charcoal production in mopane woodlands at the village scale. Our study provides new knowledge on the relationship between charcoal production and biodiversity and contributes to the wider understanding on how land use intensification is organising global biodiversity.

Specifically we investigated the following questions:

(a) Species response: Which species increase or decrease in occurrence ('winners' and 'losers') due to charcoal production?

(b) Biodiversity change: How do alpha (species richness) and beta diversity (pairwise dissimilarity in species composition) change in response to charcoal production?

We discuss our results in the context of ecosystem services provided by mopane woodlands to rural people, and compare the impact of charcoal production with that of other drivers of biodiversity change in the region.

Methods

Approach

We used 'space-for-time' substitution in this study, assuming that spatial variation in the ecological communities that we studied is a result of differing temporal land use and landcover change history. For each community of each taxonomic group we collected occurrence data, which took the form of counts for trees and ground beetles (hereafter 'beetles') and incidence for mammals. We analysed multi-species occurrence using hierarchical meta-community models (Dorazio *et al.*, 2005) in a Bayesian framework employing Markov Chain Monte Carlo (MCMC) simulation.

Study area

We conducted this study from August to October 2014 in the Mabalane district of Gaza province in southern part of Mozambique. This area is a mopane woodland-dominated dry tropical landscape situated in the flood plains of the Limpopo River and between the Banhine and Limpopo national parks (Figure 1).

The area is a charcoal production hotspot and has seen a noticeable increase in charcoal land use in last 10 years mainly to meet the increasing demands of charcoal from Maputo, the capital city of Mozambique (Luz *et al.*, 2015; Baumert *et al.*, 2016). Charcoal production is the primary cash generating activity in rural areas, accompanied by low intensity subsistence farming (mainly of maize) and livestock grazing. The charcoal industry in Mabalane has overexploited a number of areas and has been exploring new frontiers. This has resulted in a gradient of villages representing different stages of charcoal production, from villages where the charcoal production is yet to start commercially, through villages where charcoal production has just begun, to villages where charcoal production has surpassed the limit of woody-biomass, with new charcoal areas at increasing distances from Maputo.

Village selection and intensity classes

We selected six villages in a chronosequence representing a gradient of intensity of charcoal production, and ranked them from 1 to 6 in increasing order of intensity (Table 1). We determined the intensity on the basis of (i) time since the charcoal production started and (ii) time since the highest production in the village (Table 1). Our selection of chronosequence is identical to the other studies in the same area (Baumert *et al.*, 2016; Woollen *et al.*, 2016).

Table 1: The selected villages representing the charcoal land use gradient from low to high (intensity classes: 1 to 6) and the criteria of selection.

Selection criteria	6	5	4	3	2	1
Year when charcoal production started	1996	1996	1996	1998	2004	not yet (2014)
Year when charcoal production peaked	2006	2009	2013	2014	not yet (2014)	not yet (2014)

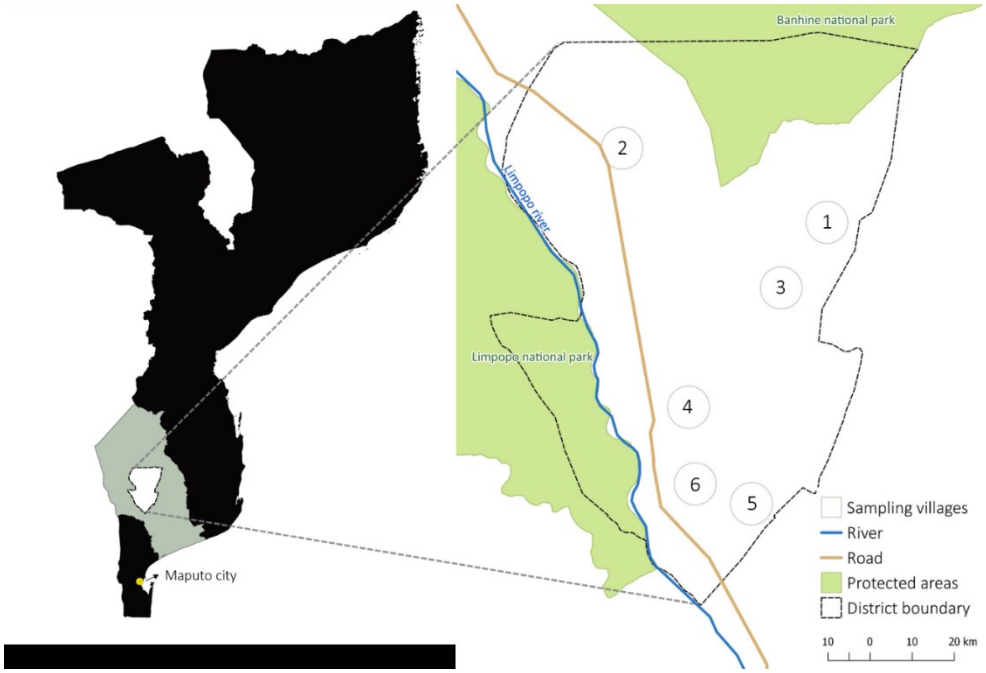


Figure 1: The Mabalane district (in white), Gaza province (grey) in Mozambique. The study villages are coded from 1-6 with the 5 km radii from center as sample area. The villages represent a chronosequence of charcoal production intensity from low (1) to high (6)

Diversity data collection

An area encompassed by a 5 km radius from the centre of each village comprised a sampling area (Figure 1). The centre of the village was defined as the community meeting point in each village following Woollen et al. (2016) who conducted the vegetation diversity study and performed land cover classification in the same study area. Within the sampling area of each village we collected species-level data for trees, beetles and terrestrial ground-dwelling mammals using circular plots, pitfall traps and belt transects, respectively. The tree data in each village were collected using 24 randomly selected circular plots of 20 m radius. Within each plot, the diameter at breast height (DBH) of all tree stems (DBH > 5cm) was measured, and the stems were identified by their local names, with assistance from local village experts. The unidentified stems were collected, identified using the morphology based taxonomy keys in Palgrave *et al.*, (2002), and along with the local names of known stems, were assigned scientific names using field guides. The stems that could not be identified were treated as distinct unknown species and given unique

codes. We further cross-validated our identification by showing the collected specimens to the botanists at the University of Eduardo Mondlane in Maputo.

The ground beetle sampling was performed within 20 m of the centre of the tree plots. We placed 10 pitfall traps at 2 m intervals in a single line in a randomly chosen direction for 3 days. The traps were made by using 10 cm tall and 7 cm wide plastic cups dug in to the ground, with the rim at ground level, and filled with 30 ml water and a drop of powder detergent to break the surface tension. We divided the traps into two sets of 5 and considered each set as a detection replicate. After 3 days, the insects caught in the traps were collected, counted and classified into morphologically distinct groups (operational taxonomic units - OTUs) and assigned numeric codes. The total number of individuals from each OTU in each trap set was recorded. One representative sample from each OTU was collected for further taxonomic classification. These OTU samples (hereafter termed 'species') were morphologically matched with specimens in the Natural History Museum in Maputo and were assigned scientific names of the morphologically closest specimen in the museum collection.

The ground-dwelling mammal species were sampled by undertaking sign surveys using 12 belt transects of 500 m length and 2 m width in each village. The 12 transects comprised three transects in each cardinal direction placed at least 500 m away from each other. Each belt transect was further divided in to two segments of 150 m length with a distance of 200 m between them. The two segments within each transect were used as a spatial detection replicate. Since the belt transects were just 500 m away from each other and a number of the mammal species that we encountered in our study may have ranges greater than 500 m in diameter, we were potentially sampling and estimating activity of those mammals in the transect instead of their absolute presence. However, we still consider this to be informative, as activity is often correlated with occupancy and population size (Efford *et al.*, 2012). In each segment of the transect we noted down all the possible signs of mammal species that we encountered, from pug marks, spoor, scats and dens to

signs of feeding. We took help from local hunters to assign the signs of mammals we encountered to their local names. We also asked them to point out the photograph of the mammal that resembles their identification in photographic field guides (Liebenberg, 2000; Gutteridge *et al.*, 2013). We further cross-checked identification of signs by different hunters in different villages. The signs that could not be identified but seemed consistently distinct were assigned numerical codes and considered as individual, unidentified species.

Landcover and woody biomass

To account for variation in landcover and woody biomass, we identified the dominant landcover and estimated the mean biomass in a 100 m buffer around the sampling unit of each taxonomic group.

To identify the dominant landcover, we used a supervised landcover classification which was based on Landsat and radar satellite images (Woollen et al. 2016). The classification identified five major landcover classes: Mopane, Shrub-Mopane, *Combretum* woodland, *Boscia* woodland and *Androstachys* forest. Androstachys forests are dense forest systems with almost no grass biomass and are categorised by the dominance of *Androstachys johnsonii*. Mopane woodlands are *C. mopane*-dominant systems, while Shrub-Mopane woodlands are characterised by *Aloe spp.* and *C. mopane* trees of smaller sizes (2 m height). The *Combretum* woodlands are mixed species and *Boscia* woodlands are *Boscia*-dominated open systems. In our analysis, we merged the structurally and floristically similar *Combretum* and *Boscia* woodlands as Open-woodlands to reduce the number of parameters.

To estimate above-ground biomass of sampling units, we produced an above-ground woody biomass map (tC ha^{-1}) of November 2014 at 25 m resolution using images obtained by the Phased Array L-band Synthetic Aperture Radar sensor on the Advanced Land Observing Satellite (ALOS PALSAR) and following the methods described in Ryan et al. (2012). To quantify the accuracy of the biomass map, we compared and validated the biomass estimation from the map with the

woody-biomass measures calculated from the vegetation plots following Ryan et al. (2011). The biomass map used in this study thus had an accuracy of 0.34 (R^2).

Data analysis

We described and made inferences at the three hierarchical levels of ecological communities: meta-community, community and individual species. A meta-community is defined as a set of local communities linked by dispersal and source sink dynamics (Leibold *et al.*, 2004) and a community is defined as a group of organisms belonging to multiple species living in a specific space (Vellend, 2010)

We assessed survey completeness by estimating the meta-community size i.e. the total species richness following two methods: (i) Hill number and sample-based rarefaction and extrapolation of species (Chao et al. 2014; Hsieh et al. 2016) and (ii) estimation of total species from hierarchical meta-community models, which we will discuss below. For the community state we used indicators of community-level response: the species richness (alpha diversity) and species composition (beta diversity); for species state we used species occurrence: abundance in the case of trees and beetles, and incidence for mammal species.

In this study, we examined the community and species state of the three taxonomic groups we investigated. We identified appropriate models for each of the state variables and investigated the relationships between the state variables and the predictor variables of charcoal intensity, biomass and landcover type, using the hierarchical model framework. We explain these models for each of the taxonomic groups below:

Species state

For trees, we had two measures of species state: the abundance (count) and the basal area. We modelled abundance as a Poisson process, and basal area as a log-normal distribution. Beetle abundance data were also in the form of counts, and were therefore also modelled as a Poisson distribution. Mammal species state were

observed as incidence from the sign surveys and therefore we modelled mammal species as a Bernoulli process.

We assumed that tree species have homogeneous and perfect detection within a sampling unit. However, there may be heterogeneity at the level of the total study area stemming from the variation between sampling units. We took this sample-driven variation into account by estimating the sampling unit-level probability of detection, which is fundamentally the probability of occurrence. Thus, we modelled tree counts using a Binomial-Poisson regression based on the Dorazio/Royle/Yamaura (DRY) model (Yamaura et al., 2012).

For beetles, the number of individuals caught in each trap is the observed part of the true abundance, a latent variable. Ground beetle species may have a variation in trap response (detection heterogeneity/ imperfect detection) which may influence and bias the number of individuals between species. We used the DRY model with zero-inflation, which is fundamentally a Binomial-Binomial-Poisson model accounting for variability in detection between the replicated trap and also for the habitat suitability through zero-inflation.

To estimate occupancy of mammal species we used the Dorazio/Royle (DR) community occupancy model (Dorazio *et al.*, 2005, 2006) and accounted for heterogeneity in detection by undertaking spatially replicated surveys on the two 150 m segments within each transect. Since we employed space-for-time substitution, and the spatial replicates are not random but in a straight line, we suspect that our detection may be spatially correlated, i.e. a species found in segment one is more likely to be found in segment two. Following Hines et al. (2010) and Whittington et al. (2015), we modelled this as an autoregressive observation state by decomposing the process of detection into two components: (1) p=probability of detection when the species was not detected in previous segment and (2) p'=probability of detection when species was detected in previous segment.

This multilevel model for estimating occupancy of mammals thus now becomes a first-order spatial Markov process (Hines *et al.*, 2010).

To account for dependence between species, we treated species-specific effects as random by drawing them from a common distribution. We relied on the assumption that species-specific effects are stochastic and exchangeable – "*similar although not identical*" (Kéry *et al.*, 2012, 2016). Therefore, all the models that we employed for analysis of species occurrence are fundamentally multilevel mixed effects hierarchical models.

Community state

We computed two community-state parameters: (i) species richness (SR), and (ii) mean community dissimilarity (MCD) – a measure of variation in community composition, or beta diversity. The MCD is equivalent to the Local Contribution to Beta Diversity (LCBD) by Legendre & De Cáceres 2013. Communities can change in species composition due to two processes: (i) replacement of species and thereby turnover in the community, and (ii) loss of species with low or no turnover and thereby nestedness in the community. We computed both the turnover and the nestedness components of the multi-part Sorenson dissimilarity following Baselga (2010).

The community-state parameters were estimated as posterior means from the detection-corrected matrix of species occurrence. The community estimates derived from the posterior distribution consist of two related estimates, the mean and standard deviation of the estimated mean. We modelled the posterior mean estimates using a simple regression and propagated the estimation uncertainty by constructing two residual components. The first component is the known uncertainty based on the posterior standard deviation of the estimate, and second residual component is the lack of fit from the simple regression model.

Model analysis and inference

We analysed the above mentioned models in a Bayesian framework. We chose Bayesian analysis because fitting the meta-community model (which makes inferences at the three hierarchical levels – meta-community, local community and species – in the same framework) is more easily performed with a Bayesian than a frequentist approach. Complex models are easy to construct in the BUGS language with more flexibility and reproducibility. Maximum likelihood estimations in the frequentist framework are based on asymptotes needing more data than the simulation based Bayesian framework. In the Bayesian framework uncertainties can be easily propagated in to the models (Kéry *et al.*, 2012).

We specified the models in BUGS language and executed simulations using three markov chains, each composed of 75,000 iterations, of which the first 25,000 were discarded as 'burn-in'. The thinning rate was set to 50, yielding 3,000 samples from the posterior distributions.

Our objective in this study was to test relationships between ecological responses (species and community state) and land use-landcover variables (intensity, mean biomass and landcover type), so the species and community models were built with land use-landcover variables as predictors in a linear combination. To reduce number of parameters, we converted the categorical village levels into an ordinal variable (from 1 to 6, with 1 representing the lowest and 6 the highest level of intensity).

We constructed four species-state (occurrence) models – two for trees (count and basal area) and one each for beetles (count) and mammals (incidence) – and three community-state models (alpha, beta-turnover and beta-nestedness) for each taxonomic group. We checked all the models for convergence using the Gelman-Rubin convergence diagnostic (Gelman *et al.*, 1992) with potential scale reduction factor (PSRF) values approaching 1 (and no higher than 1.1) considered acceptable.

We used the 95% Bayesian Credible Interval (CI) to indicate significant effects; if the bounds of the 95% CI did not contain zero, the effect was considered significant.

Since this study is a spatial comparison, the explanatory variables and dependent variables are likely to be spatially auto-correlated (Diniz-Filho et al., 2003). To test and quantify the spatial autocorrelation we used Global Moran's I, one of the commonly used measurements of spatial correlation (Chen, 2013). We examined the spatial autocorrelation in the mean species richness of trees, mammals, and beetles, and intensity class of charcoal production. The Moran's I ranges from -1 to 1 indicating dispersion (negative correlation) and clustering (positive correlation) respectively.

Details of models

(a) Occupancy models: In the hierarchical occupancy models, which consisted of three levels (species occupancy, community size and meta-community size), we used heterogeneity in detection probability among species to inform estimations at each level and derive detection-corrected estimates (MacKenzie *et al.*, 2002). Species-level detection sits at the bottom of this hierarchical layer. It informs the probability of a site (sampling unit) being occupied (occupancy). The variability in occupancy and detectability among species is further used to estimate the true number of species in a community and the total number of species that may be present in the overall study area (the super population or the meta-community size). Our sampling is unlikely to contain all species that may be present in the study area, but an estimate of the unobserved true meta-community size can still be made by data augmentation, where the encounter histories of observed species are augmented with encounter histories of unobserved species represented by zeros. The unobserved species are M-n, where n is the observed and M is the expected number of species, the latter of which can be derived from a secondary source, such as a literature review or regional checklists.

The models that we used in this study are essentially the single-season, single-species site-occupancy models (MacKenzie *et al.*, 2002) which are extended to take into account multiple species (by treating species-specific parameters as random effects; Dorazio & Royle 2005; Dorazio et al. 2006) and unobserved species (by data augmentation; Kéry & Royle 2009; Royle et al. 2007).

Following the concept of data augmentation (Royle et al. 2007a), we identified the full number of species that we expected to find in the study area (N=150 for trees and 100 each for beetles and mammals) and augmented our data set with "all zero" encounter histories of those species which weren't detected. The data augmentation gave us an estimate of true meta-community size, which is equivalent to asymptotic richness (Kéry *et al.*, 2009). We provide details about the parameters in the models in Table 2.

Table 2: The hierarchical occurrence models accounting for detection for the three taxonomic groups

Taxonomic group	Trees	Beetles	Mammals
Super population process		$w_k \sim \text{Bernoulli}(\Omega)$	
State process: occurrence	$N_{ik} \mid a_{ik} \sim \text{Poisson}(a_{ik} \lambda_k)$	State processes 1: (suitability) $a_{ik} \sim \text{Bernoulli}(w_k \Phi_k)$ State processes 2: (abundance) $N_{ik} \mid a_{ik} \sim \text{Poisson}(a_{ik} \lambda_k)$	$z_{ik} \mid w_k \sim \text{Bernoulli}(w_k \Psi_k)$
Observation process: detection	$Y_{iik} \mid N_{ik} \sim \text{Binomial}(N_{ik}, p_{ijk})$	$Y_{iik} \mid N_{ik} \sim \text{Binomial}(N_{ik}, p_{ijk})$	$Y_{iik} \mid z_{ik} \sim \text{Bernoulli}(z_{ik} p_{ijk*} p'_{ijk})$
Models of species heterogeneity in occurrence	$\log(\lambda_{ik}) = \beta 0_k + \beta 1_k$ * Intensity + $\beta 2_k$ * biomass + $\beta 3_k$ * landcover	$\log(\lambda_{ik}) = \beta 0_k + \beta 1_k$ * Intensity + $\beta 2_k$ * biomass + $\beta 3_k$ * landcover	$\text{logit}(\Psi_{ik}) = \beta 0_k + \beta 1_k$ * Intensity + $\beta 2_k$ * biomass + $\beta 3_k$ * landcover
Detection heterogeneity in detection	$\text{logit}(p_{ijk}) = \alpha 0_k$	$\text{logit}(p_{ijk}) = \alpha 0_k + \alpha 1_k$ * biomass	$\text{logit}(p_{ijk}) = \alpha 0_k + \alpha 0_{ylag k}$ * $y_{i,j-1,k}$ + $\alpha 1_k$ * observer + $\alpha 2_k$ * biomass

For all the taxonomic groups, k is the index of species which runs from 1 to M (expected number of species). The Ω is the meta-community occupancy or the super-population parameter and helps in estimation of N because $N=M\ \Omega$, the unobserved estimate of meta-community size. The data augmentation variable w_k represents the sampling process and indicates the probability that the species is part of the super-population. The true occurrence of species (trees and beetles=N_{ik}; mammals=z_{ik}), another latent variable, is conditional upon the data augmentation variable w_k. The true occurrence is modelled as a Poisson distribution for trees and beetles with probability of abundance λ_k and as a Bernoulli distribution for mammals with probability of occurrence Ψ_k. For beetles, an additional level a_{ik}, a habitat suitability parameter which is modelled as Bernoulli trial, is introduced between the data augmentation variable (w_k) and true occurrence (N_{ik}) to account for zero-inflation.

The observed data Y_{iik} which is conditional upon the unobserved latent state (trees and beetles=N_{ik}; mammals=z_{ik}) is simulated as a random variable with probabilities of occurrence which is the product of the observed occurrences and detections probabilities. For trees and beetles, the observed count of individuals of species k at site i is modelled as a Binomial trial with a probability that is the product of the abundance of species k at site i and the detection probability of species k during survey occasion j at the site i. For mammals, the observed incidence of species is modelled as a Bernoulli trial with probability of occupancy which is the product of the incidence of species k at site i and the detection probability for species k during survey occasion j at the site i. The detection of mammal species in this study follows a Markov process, where the spatial replicates are autoregressive. The detection probability of mammal species is a combination of p and p'. For the first segment, we used a weighted mean detection p_μ, which can be calculated as $p_\mu = p/(p+ (1-p'))$.

The occurrence probability (λ_k) for trees and beetles and mammals (Ψ_k) is modelled using the predictors intensity, biomass and landcover type in linear combination

with β1, β2 and β3 as respective beta coefficients and β0 as the intercept. The detection probability of trees is homogenous and contains only the intercept ($\alpha 0$). The detection probability of beetles consists of biomass as a predictor as the quantity of biomass (high biomass = tree-dominated, low biomass = grass/herb-dominated) around the trap set can influence the trapping rate. The detection probability of mammals contained observer and segment-level biomass as predictors, with $\alpha 1$ and $\alpha 2$ as their respective coefficients. We assumed that the skill set of observers and biomass around the transect influence mammal detection. For both detection and occurrence, the species-specific parameters are constrained and drawn from a common normal prior distribution.

Therefore, $\boldsymbol{\beta_k \sim Normal\ (\mu_\beta\ \sigma^2_\beta),\ \ \alpha_k \sim Normal\ (\mu_\alpha\ \sigma^2_\alpha).}$

(b) Community-state models: Using the detection-corrected estimates of species occurrence from the hierarchical models, we computed the community-state variables, species richness, the turnover component of beta diversity and the nestedness component of beta diversity. The variables have two related parameters: the posterior mean and standard deviation. We modelled the c^{th} community variable at site i (A_{ci}) as a normal distribution with mean (μ_{ci}) and known standard deviation (σ^2_{ci}). We then used the mean (μ_{ci}) of this distribution in a regression model as the response variable with predictors in additive combination and residual error, ε_c.

$$\boldsymbol{Aci \sim Normal\ (\mu_{ci}\ \sigma^2_{ci})} \quad (1)$$

$$\boldsymbol{\mu_{ci} = \beta 0_c + \beta_c * Intensity_i + \beta 2_c * landcover_i + \beta 3_c * biomass} + \varepsilon_c \quad (2)$$

R packages and functions

We computed the sample-based total species richness, accumulation and survey completeness using the *iNEXT* package (Hsieh *et al.*, 2016). We used the *adespatial* package to calculate the turnover and nestedness components of beta diversity. To fit the Bayesian models specified in BUGS language we used the *jagsUI* package

(Kellner, 2015). For constructing the meta-community models in R, we used code provided by Kéry & Royle (2016) and Kéry & Schaub (2012). Figures were drawn using *ggplot2* (Wickham, 2009).

Results

Our complete data set contained a total 709 mammal signs, 15,393 tree stems and 1822 ground beetle individuals belonging to 41, 98 and 48 species, respectively. For mammals and trees, we achieved more than 95% completeness in species accumulation, while for the ground beetles at the figure was 91 %. The extrapolated sample-based species richness estimates without accounting for detection heterogeneity were lower than the detection corrected total estimates from the hierarchical models (Table 3).

Table 3: Summaries of meta-community and community states of the three taxonomic groups derived from observed data, sampled based extrapolation and model derived posteriors.

	Trees		Mammals		Beetles	
	mean (n=136)	95% CI	mean (n=71)	95% CI	mean (n=135)	95% CI
Plot-level mean species richness	5.3	5.2 - 5.4	6.1	5.9 - 6.3	1.84	1.78 – 1.89
Beta diversity	92.6	92.5 - 92.8	34.9	34.7 - 35.1	46.15	46.1 - 46.2
Observed total species richness	98		41		48	
Sample based estimate of total species richness	141.2	114 - 212	42	41 – 49	70	55.5 -113
Detection corrected estimate of total species richness	144	130 – 150	60.4	46 - 86	91.36	73-100
Sample completeness	0.96		0.98		0.91	

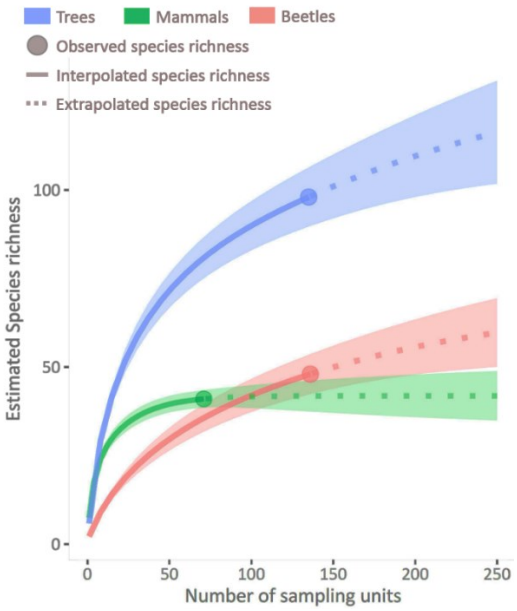


Figure 2: The interpolated and extrapolated sample based species accumulation curve with 95% confidence interval of the three sampling groups.

Across the study area the dominant trees were *Androstachys johnsonii* (relative abundance=0.27), *Colophospermum mopane* (0.23) and *Guibourtia conjugata* (0.12); the dominant mammals were common duiker, *Sylvicapra grimmia* (naïve occupancy=0.12), Scrub hare, *Lepus saxatilis* (0.11) and Steenbok, *Raphicerus campestris* (0.09); and dominant beetles were *Pachylomera femolaris* (relative abundance = 0.78), *Macrocerus spp.* (0.06) and *Cypholoba spp*. (0.05).

10 Effect of charcoal production intensity on species- and community-level occurrence

Community-level occurrence:

Our results show that land use intensity had significant negative effects on the average community-level occurrence of mammals and trees, but no significant effect on that of beetles (Figure 3). The mean community-level occurrences (CO) of mammals (mean± SD, occupancy, $\Psi = 0.91 \pm 0.9$) and trees (abundance, $\lambda tr = 0.55 \pm 0.6$) were reduced by 34.5 % (SD ± 0.5) and 21.5 % (SD ± 0.8), respectively, with increasing levels of charcoal land use intensity (intensity) from class 1 to 6. In addition, biomass was positively correlated, while Androstachys woodlands and

shrub-mopane were associated with reduced tree CO. The CO of beetles was significantly increased by 23.5 % (SD ± 0.07) in open woodlands. The shrub-mopane and Androstachys habitats had reduced CO of beetles, however it was significant only at 90% CI.

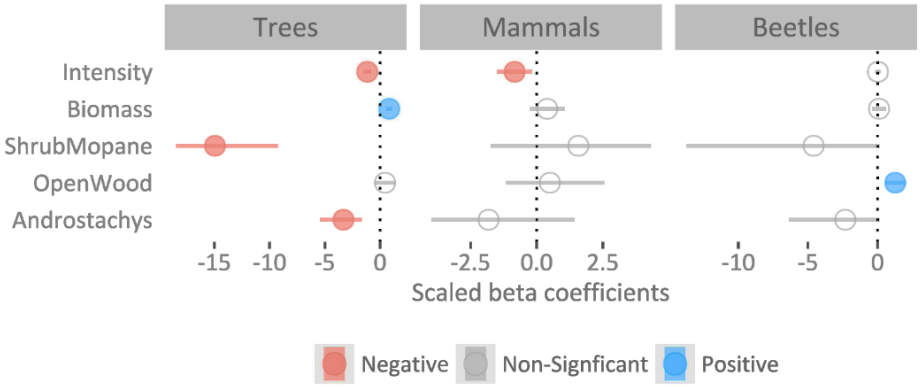


Figure 3: Land use intensity had a negative effect on community-level occurrence of mammals and trees. The community-level average population size of trees was lower than the study mean in the Androstachys and Shrub-mopane habitats. The open woodlands had higher average populations of beetle communities. The circles denote beta coefficients, the horizantal lines represent 95% CI and colours indicate direction of relationship of landcover-land use variables and taxonomic groups.

Individual species-level occurrence

Trees

At the individual species level, charcoal production intensity had a disruptive effect on trees, reducing the population size of a majority of species. This suggested the existence of a *more losers than winners* phenomenon (McKinney *et al.*, 1999; Tabarelli *et al.*, 2012) in high charcoal-intensity areas. In addition, biomass was positively correlated with most species. The abundance of most tree species significantly increased in open-woodlands and declined in *Androstachys* and shrub mopane habitats (Figure 4).

In response to increasing intensity, the abundance of 44 tree species significantly declined, while that of 14 significantly increased; the rest showed non-significant responses. Among the negatively affected, *C. mopane,* the preferred tree species for charcoal production (charcoal species) did not reduce in abundance and instead increased in high intensity areas by 2.8 % (±0.2).

However, when stem area was taken in to consideration *C. mopane* decreased by 5.7 % (±2.7) albeit non-significantly. Another charcoal species, *Xeroderris stuhlmannii*, followed a similar trend to *C. mopane*, increasing in abundance (4.7 % ± 0.2) but declining (7.9 % ± 3.4) in stem area.

The abundance as well as the stem area of other charcoal species in the region (according to Woollen et al. 2016) – *Acacia nigrescens, Combretum spp., Guibourtia conjugata, and one* unidentified species, locally called *Lumanhama* – declined with intensity. The other negatively affected species consisted mainly of timber-fire wood species such as *Balanites maughamii*, *Hymenocardia ulmoides, Afzelia quanzensis, Berchemia discolour, Ptaeroxylon obliquum, Albizia petersiana, Kirkia acuminata* and *Diospyros loureiriana*, or fruit-medicine species such as *Croton pseudopulchellus, Suregada zanzibariensis, Salvadora persica* and *Adenium multiflorum* (Louppe, D., Oteng-Amoako, A.A., 2008; PROTA, 2013). The positively associated species consisted of more shrub-scrub habitat-preferring or disturbance-tolerant secondary-growth species such as *Acacia nilotica kraussiana, Acacia burkei, Boscia spp* and *Diospyros mespiliformis* (PROTA, 2013).

Biomass had a positive effect on most tree species, with 31 species increasing and only six declining in abundance as biomass increased. In open woodlands, majority of species (increase, I = 29, decrease, D = 15) significantly increased in abundance (compared to the study site average). The shrub-mopane and *Androstachys* woodlands, being species-poor systems, were associated with more species decreases than increases (shrub-mopane: I = 1, D = 28; *Androstachys*: I = 11, D = 24). The shrub-mopane especially was represented by only one species, *Aloe marlothii orientalis* which is a drought-resistant and a fast-growing species of dry arid areas (PROTA, 2013).

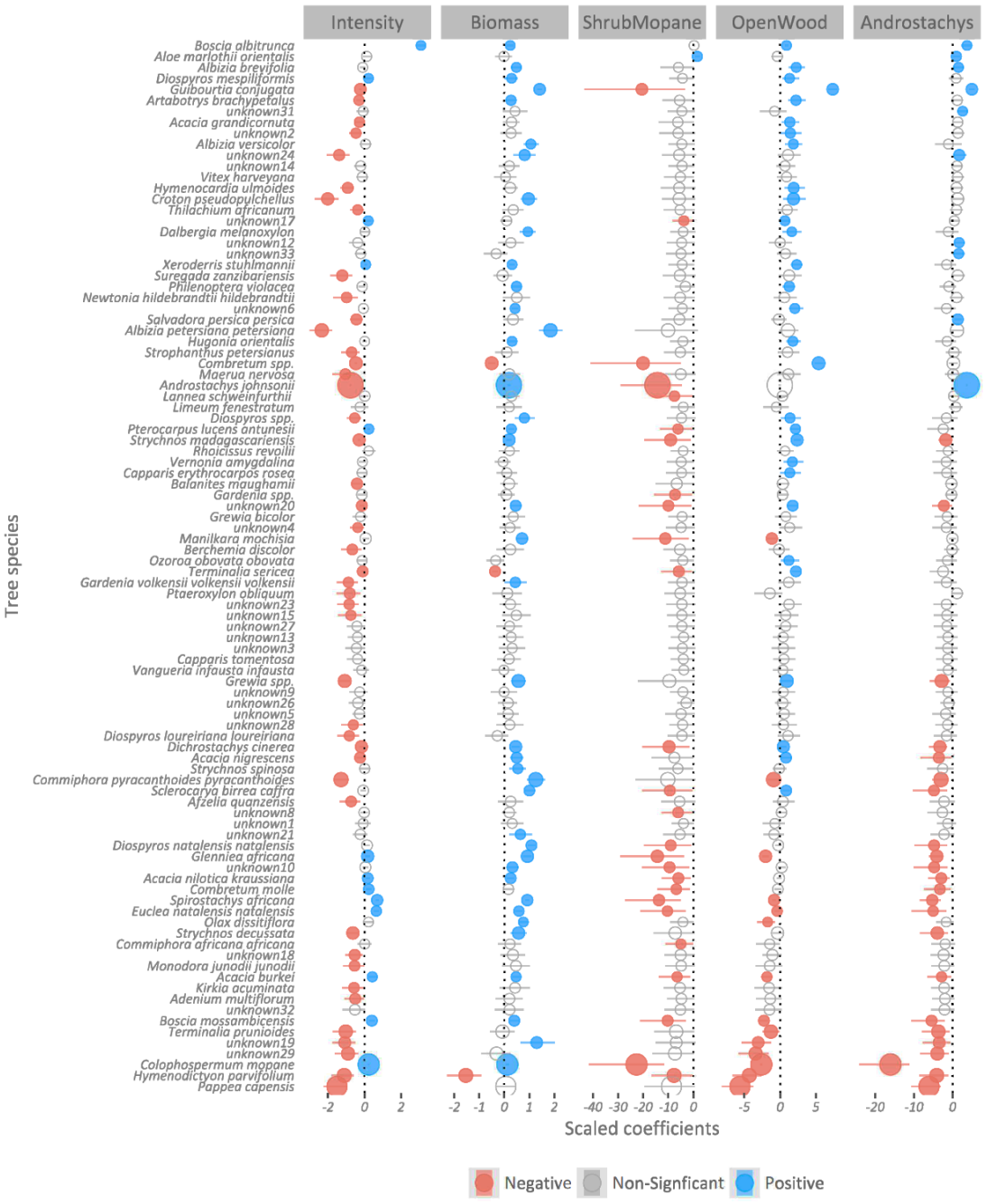


Figure 4: The beta coefficients representing effects of intensity, biomass and landcover on abundance of tree species demonstrate the negative effect of intensity on majority of tree species leading to more species losses and fewer gains. Biomass and open woodland landcover were associated with higher, while shrub mopane and androstachys landcover were related to the lower populations of majority of species. The positions of the circles represent scaled beta coefficients (per unit standard deviation), horizontal lines show 95% CI, colours indicate direction of effect, and the sizes of circles denote the relative abundance of species.

Mammals

The occupancy models for mammals showed a high probability (0.9) of occupancy for most species (Figure 5a), suggesting that almost all of the species encountered during the study were found throughout the study area. The mean detection probability (0.23), which was a composite of *p* and p' (Figure 5b) showed high heterogeneity (SD = 0.27), ranging from 0.04 to 0.8. The detection probability significantly varied between the two observers (mean observer effect, 0.46 ± 0.21) and increased with segment-level biomass (biomass effect, 0.33 ± 0.17), affecting detections of 9 and 1 species, respectively.

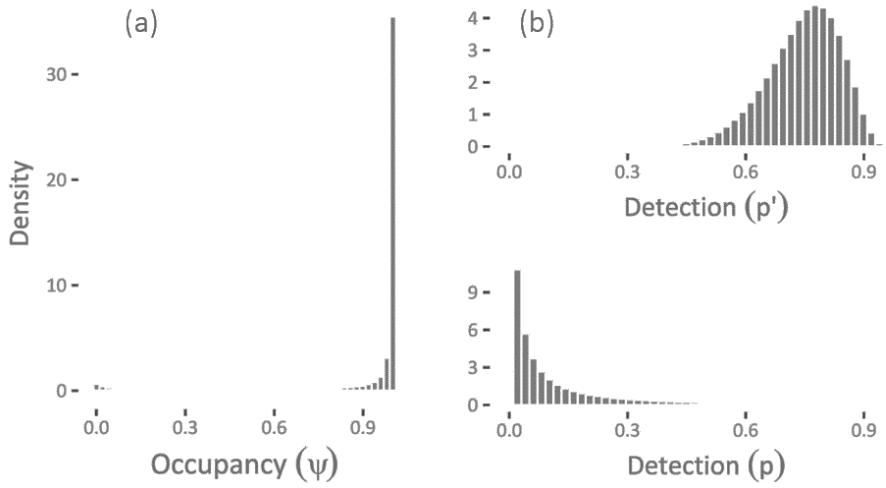


Figure 5: Distribution of community-level mean of occupancy (Ψ_μ) and detection probability (p and p') based on occupancy and detection parameters derived from the hierarchical single season occupancy model with markovian detection showing high probability of occupancy (mean=0.91) but with low and heterogeneous detection.

The average occupancy probability of mammal species reduced with increasing levels of intensity. However, among the 41 species that we recorded during this study, the negative effect of intensity was statistically significant at 95% CI for only three species: Nyala, *Tragelaphus angasii* (-0.4 ± 0.16); springhare, *Pedetes capensis* (-0.3 ± 0.1), and Aardvark, *Orycteropus afer* (-0.3 ± 0.1). Within 90% CI bounds, occupancy probabilities of four other species showed reduction in response to increasing intensity (Figure 6). Shrub-mopane had higher occupancy of Aardvarks (0.9 ± 0.4).

Open woodlands had higher occupancies of Aardvarks (0.5 ± 0.3), springhares (0.6 ± 0.3) and striped weasels, *Poecilogale albinucha* (1 ± 0.5).

Beetles

Among beetles, the community-level mean occurrence and detection was low and highly variable (abundance: λgb= 0.6 ± 0.4, detection: *p=0.11 ± 0.07*). Of the 48 species observed in this study, nine showed a significant response to any of the predictors in the model with eight increasing and one showing a reduction. *Pachylomera femolaris,* the sole decreasing species, was reduced in *Androstachys* woodland. The abundance of seven *(Cypholoba capilliaudi ssp. planti, C. capilliaudi ssp. Ranzanii, C. gracilis, Ddontegnathis fulvipennis, Genecephallum veigaii and Graphopterus velutinus)* increased in open woodlands, one (*Adoretus strigatus)* increased in *Androstachys* and one (*Cypholoba capilliaudi ssp. ranzanii)* increased with intensity. The coefficient plot of beetles is provided as supplementary material.

The results of species-level response suggest that a greater number of tree and mammal species reduced than increased in occurrence in response to charcoal intensity. For beetles, landcover was more important than intensity.

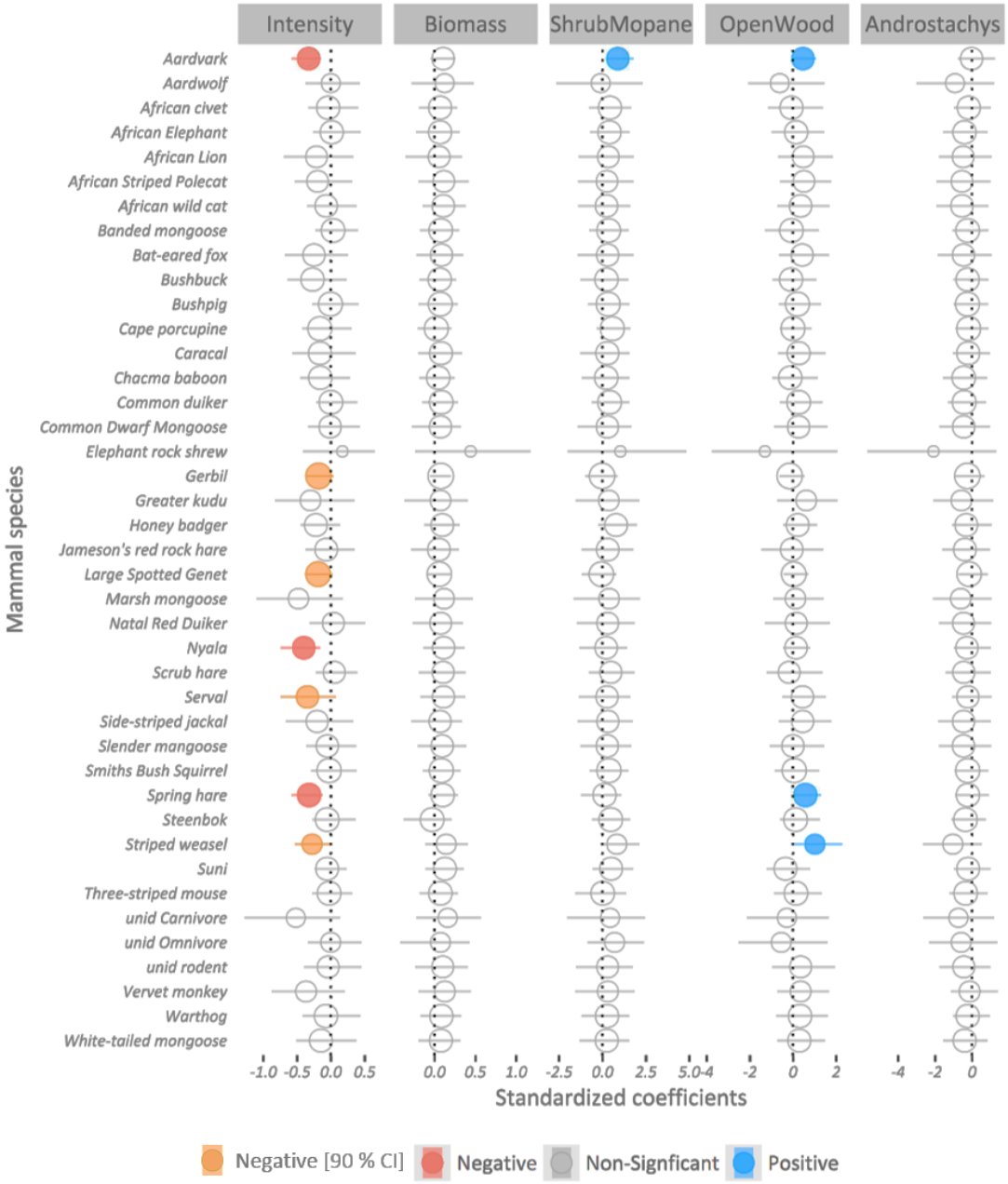


Figure 6: The beta coefficients of charcoal land use intensity, biomass, and landcover types in the hierarchical occupancy model show negative effects of intensity on occupancy probability for three species at 95% CI and an additional four species at 90% CI. The positions of the circles denote standardized coefficients (proportion of variance from the mean), the horizontal lines indicate 95% CI, and colours indicate direction of effect. The sizes of the circles represent probability of occupancy on logit scale.

Effect of charcoal land use intensity on the community state: alpha and beta diversities

Among the community-state parameters, tree and mammal species richness decreased with intensity, but beetle species richness showed no significant response. Under increasing intensity, the turnover component of beta diversity significantly reduced for trees and increased for mammals while the nestedness component increased for trees and reduced for mammals. Landcover – but not intensity – had a significant effect on beta diversities of beetles (Figure 7).

With each increasing level of intensity, the estimated tree species richness (SR=35.2 ± 2.5) and beta diversity (MCD=0.8 ± 0.02) reduced by 12% (± 2) and 19.5% (± 0.1) respectively. With reduction in community size and dissimilarity, the tree communities increased in community nestedness (MND=0.1 ± 0.02) by 85% (± 10). Biomass was correlated with increased species richness of trees. The number of species was higher in open-woodlands and lower in shrub-mopane and *Androstachys* land covers. The turnover of tree communities increased with biomass but decreased in open woodlands and did not change significantly in other landcovers. The shrub-mopane and *Androstachys* woodlands contained more nested tree communities.

Estimated mammal species richness 52.5 (±4.7) reduced by 8.5 % (± 4) for each increasing level of intensity. Mean community dissimilarity 0.02 (± 0.01) in species composition i.e. species turnover increased by 98 % (± 40) and the average nestedness 0.15 (± 0.01) reduced by 15.5 % (± 4) in response to each increasing level of intensity. In *Androstachys* woodlands, mammal communities had lower species richness and nestedness but a higher turnover than the study average. Biomass and other landcover variables did not have any significant effect on diversity of mammal communities.

Beetle species richness (4 ± 0.7) did not significantly vary with intensity. The open woodlands had significantly higher species richness (66 ± 10 %) and turnover (24 ± 7 %) than the study average. *Androstachys* forests were also associated with significantly higher turnover (79 ± 17 %) than the average while nestedness significantly increased (5.8 ± 2.5 %) with biomass.

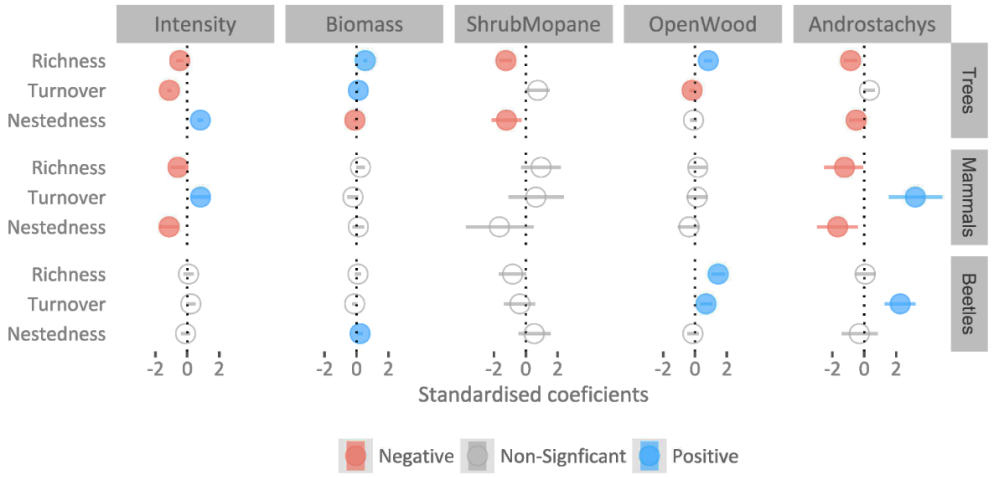


Figure 7: The scaled coefficients (circles on x-axis) with 95% CI (horizontal lines) derived from the community-state models for each taxonomic group (trees, mammals and beetles) show the effect of explanatory variables (Intensity, biomass, and landcover types: shrubmopane, open woodland, Androstachys) on community parameters (species richness and turnover and nestedness aspects of beta diversity). The species richness of mammals and trees show reduction with increase in intensity. Tree communities reduce in beta diversity and become more nested while mammals increase in beta diversity and thereby show reduced nestedness in response to increasing levels of intensity. In addition to intensity, landcover was significant determinant of alpha and beta diversity of trees. Beetle communities were not affected by intensity but were structured by landcover type.

Spatial autocorrelation

The mean species richness of trees and mammals and the intensity of charcoal production showed significantly positive spatial auto-correlation (Moran's I= 0.77, $p<0.01$). The effect of intensity of charcoal production on diversity was confounded with geographical distance. With increase in distance from the village with highest intensity of charcoal production, the species richness of trees and mammals increased and that of beetles did not show any significant pattern (Figure 8a) while the intensity of charcoal production decreased (Figure 8b).

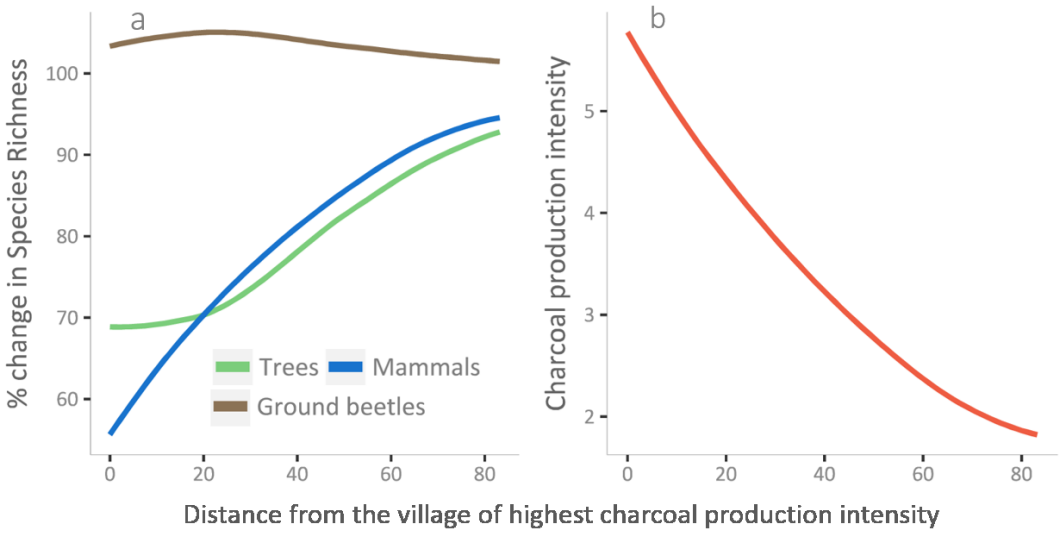


Figure 8: The species richness of trees and mammals were positively correlated with geographical distance. The sites closer to each other had similar diversity. Also, the intensity of charcoal production was spatially structured. Geographically nearer sites had similar levels of intensity. Thus, the effect of intensity is confounded with geographical distance as both, intensity and diversity, are spatially auto-correlated

Discussion

Work presented in this chapter shows that charcoal production alters diversity and composition of ecological communities. It also underlines that its effect could vary between taxonomic groups. While trees and mammals both reduced in alpha diversity in response to the intensity of charcoal production, their beta-diversity patterns were dissimilar. The beta-diversity (turnover component of beta diversity) of trees decreased, showing evidence of biotic homogenization. In contrast, beta-diversity of mammalian communities increased indicating biotic heterogenization. Beetle communities, however, showed no significant change in alpha or beta diversity.

This study uses space-for-time substitution and the explanatory – the intensity of charcoal production - and dependent variables – the diversity measures are spatially auto-correlated. Our inferences here are based on the assumption that the observed spatial patterns between ecological communities are manifestations of the increased intensity of charcoal production and not of other deterministic or random processes.

With this assumption, we place a weak causal inference on the role of charcoal production in the region. The inference here, however, hold validity because: (i) we sampled a chronosequence of villages with differences in land use over decades, whilst accounting for variation in land cover, and (ii) the sampled villages were within 100 km of each other. The ecological communities we investigated are hence expected to be similar in the absence of charcoal production. Further, commercial charcoal production along with other drivers of degradation and deforestation in the sub-Saharan Africa is known to be spatially structured. The sites nearer to the towns and big cities undergo boom-bust pattern of land use change. The villages in this study followed a similar pattern as the villages nearer to the urban centres (Mabalane town and capital city - Maputo) are more degraded and new frontiers of charcoal production are created with increasing distance from those urban centres.

Therefore, on the basis of this study we can state the following:

a. Charcoal production at individual-species level reduces the population size of a majority of species across two of the three taxonomic groups we studied, resulting in more 'losers' than 'winners'.
b. At the community level, by reducing species populations and causing local extinctions, charcoal production results in loss of biodiversity.
c. The selection processes imposed by charcoal production differ between taxonomic groups, restructuring them differently, causing biotic homogenization of tree communities and biotic heterogenization of mammals.

Below, we discuss these interrelated patterns and describe the underlying processes that may have produced them.

Species response: Ordered loss of tree species and cascading effects on mammals

Charcoal production mainly involves selective harvesting of trees, preferably *C. mopane*, or other species of higher wood densities and larger stem areas

(Chidumayo, 1993; Hosier, 1993; Chidumayo *et al.*, 2013; Philomena Kumapley *et al.*, 2016; Woollen *et al.*, 2016). Therefore, increase in intensity of charcoal production accelerates extinction risks for charcoal species. In this study we found that the six charcoal species in our study area(*C. mopane*, *Combretum spp.*, *Guibourtia conjugata, Acacia nigrescens, Xeroderris stuhlmannii* and *Lumanhama* (local name) declined in both stem size and abundance, with the exception of *C. mopane* and *X. stuhlmannii,* which increased in abundance, possibly due to regrowth after coppicing (Mapaure *et al.*, 2011; Woollen *et al.*, 2016). Among the charcoal species, *C. mopane* and *Combretum spp.* are the dominant (by basal area) tree species in the region, closely followed by *G. conjugata*. While, *A. nigrescens, X. stuhlmannii* and *Lumanhama,* not being the top 25 ranking species in the region represent the infrequent species in the tree community. The other declining trees species, in response to intensity, likewise can be ordered on the basis of their use mainly as timber or fire wood irrespective of their abundances. In other words, the declining tree species comprise of the locally dominant as well rare species. The decline of these species may be an indirect effect of charcoal production; the charcoal industry opens up areas that may then also be subject to other forms of harvest. Also, the perception (of villagers) that the area has already been degraded may lead to further exploitation or less incentive to manage it. This demonstrates the existence of non-neutral processes where the chance of extinction is not equal between species and is not driven by their relative abundances (Püttker *et al.*, 2015). Instead, the species that have charcoal value or other timber-firewood utility are selectively harvested. Under such deterministic exclusion processes, the tree communities lose the dominant as well the infrequent species and retain the few widespread species which have relatively low utility value for people. Thus the few widespread *'winners'* replace many common and rare *'losers'* leading to biotic homogenisation (McKinney *et al.*, 1999; Tabarelli *et al.*, 2012).

The changes in vegetation structure and composition due to selective logging exert bottom-up controls on faunal communities (Gandiwa, 2013). Mammals in the mopane region are known to be dependent on mopane woodlands for habitat and

food (Styles *et al.*, 2000; Kos *et al.*, 2012). Charcoal production, through selective logging, alters habitat structure and resource availability. It removes the woody biomass and transforms the mopane woodland in to a low biomass secondary growth system mainly composed of coppicing mopane stems(Woollen *et al.*, 2016). The loss of large canopy trees also alters the canopy- induced factors increasing grass dominance and understorey vegetation (Smit, 2001). The alteration in micro-habitat results in a relative influx of non-woodland species through habitat selection (Rosenzweig, 1981). The reduction in resource availability results in an overall loss of species through competitive exclusion (Abrams, 1986; Yackulic, 2016). In this study, we found evidence of competitive exclusion in mammal communities, as the majority of mammal species were reduced in likelihood of occurrence in areas of high charcoal-production intensity. In addition, we demonstrated the processes of habitat selection in beetles, as the population sizes of 31 species increased with production intensity (though only one at 95% CI and three at 90% CI significance).

Charcoal production reduces biodiversity

At the global scale species richness is known to be declining (Vellend *et al.*, 2013; Newbold *et al.*, 2014). However, at the local scales there are contradictions between the temporal and spatial comparisons. The global syntheses based on temporal assessments suggest no systematic loss (Supp & Ernest 2014; Dornelas et al. 2014; Vellend et al. 2013), whereas the studies which compared spatial assemblages showed declines in species richness in response to land use pressures (Murphy *et al.*, 2014; Newbold *et al.*, 2015). However, these global syntheses lack geographical breadth and under-represent the African savanna woodlands. Through this study, we provide a mopane woodland context to the global biodiversity-land use discourse. We show that, at the village scale, the species richness of tree and mammal communities reduced as intensity of charcoal production increased, but that of beetles did not respond significantly. Thus, we also underline that biodiversity-land use relationship has taxonomic heterogeneity. Our findings align

with other studies (e.g. Gibson *et al.*, 2011; Burivalova *et al.*, 2014 and studies there in) demonstrating the same.

In the previous section, we discussed that tree species underwent *winner-loser* replacement (WLR; (Tabarelli *et al.*, 2012) where few winners replaced many losers in response to intensity. This pattern in tree communities also explain the reduction in their species richness with the intensity. Beetle communities with just one significantly responding species showed no significant change in species richness with intensity. This observation corroborates number of space-to-time comparison of the ground beetle assemblages showing similar patterns (Ulyshen *et al.*, 2006; Hayes *et al.*, 2009; Yu *et al.*, 2017). A justification for no effect of intensity on beetle communities could be that they comprise species which have broad habitat niche, are mainly generalists and more tolerant to modifications in habitat structure (Sunderland, 1996). In contrast, mammal communities reduced in species richness with increasing intensity. This is most likely the consequence of degradation (loss of biomass) and modification (structural homogenisation) of the mopane woodland. The altered mopane woodland habitats impose bottom up control causing species to compete for the limited resource (biomass) subsequently resulting in loss of species through competitive exclusion(Segre *et al.*, 2014).

Assuming that selective logging is a main activity for charcoal production, we can compare our results with other logging-biodiversity studies. Our finding about the negative effect of intensity on alpha diversity of trees and mammals is shared by the global syntheses of effect of logging intensity on biodiversity of multiple taxonomic groups (Gibson *et al.*, 2011; Burivalova *et al.*, 2014). However, to our knowledge only one other cross-group analysis (Burivalova *et al.*, 2014) has shown mammal communities to be more sensitive to logging intensity than other groups, while the majority have reported the opposite (Gibson *et al.*, 2011; Putz *et al.*, 2012; Woodcock *et al.*, 2015). As also suggested by Gibson et al. 2011, the most plausible explanation for the observed low sensitivity of mammals in the wider literature could be the dominance of less sensitive small mammals in the studied communities. Large body

size mammals are considered more sensitive as their body size also correlates with traits that predispose them to extinctions (Cardillo *et al.*, 2005). Compared to small animals, large-bodied organisms have lower reproductive rate, smaller litter and population size, long gestation and weaning periods, and large resource requirements- food and habitat range (Promislow *et al.*, 1990). Contrasting the studied communities in the wider-literature, mopane woodlands support mega-fauna which are considered more vulnerable to local extinctions (Cardillo *et al.*, 2005). In response to the disturbance in the mopane woodlands, the mammals therefore rapidly decline, explaining the high sensitivity of mammal communities in the present study. There may be concern that the mammal response to intensity in our study is confounded by hunting pressures. However, hunting for large mammals is heavily penalised by the staff of the neighbouring national parks, and hunting for small mammals such as duikers and scrub hare is unvarying in intensity across the study sites; hunting is therefore unlikely to be a significant driver of the observed patterns. In the villages of lower as well as higher intensities the number of species and individuals that were hunted did not noticeably vary (information from the 12 local hunters in 6 villages and personal observations). However, a more quantitative approach is needed to test the effect of hunting.

Charcoal production alters species composition of taxonomic groups in dissimilar ways

We did not expect a significant increase in turnover of tree communities owing to the selective nature of harvesting for charcoal production. Even in high intensities of charcoal production, there may be losses of multiple species but still no significant change in the turnover. As expected, we did not find any evidence of drift in composition-turnover of tree communities. Instead, as the species richness of trees reduced, the tree communities underwent substitution (increase in nestedness) and spatial homogenisation i.e. reduction in beta-diversity (turnover component of beta-diversity). This pattern of community structuring, loss of alpha and beta diversity, in trees can be classified as subtractive homogenisation following the framework by

Socolar *et al.*, (2016). Subtractive homogenisation entails loss of alpha and beta diversity mainly due to replacement of rare and common species by locally common disturbance tolerant or undesired secondary growth species. Hence, WLR in case of biotic homogenisation can be specifically stated as common (winner)-loser replacement, CWLR. Alpha diversity underpins ecosystem functioning and resilience and response diversity to disturbances at the local scales (Lalibert *et al.*, 2010; Hooper *et al.*, 2012). Beta-diversity retains biodiversity at the meta-community level by maintaining communities of varying species compositions. Meta-community can be defined as *a set of local communities linked by dispersal and source sink dynamic*s (Leibold *et al.*, 2004). Source-sink dynamics refer to the spatial processes that maintain (or restore) local diversity through migration from *source* and colonisation in the *sink* (Tscharntke *et al.*, 2012). *Source* represents the communities where growth rates are higher than the meta-community average, and *sink* refers to the communities where growth rates have declined (Holt, 1985). Beta-diversity, therefore, provides spatial insurance (Tscharntke *et al.*, 2012). With biotic homogenisation, hence, resilience and spatial insurance of the tree communities to future perturbations is lost.

The mammal communities, in response to intensity, underwent ecological drift – increase in pairwise dissimilarity between communities. In other words, the turnover component of beta-diversity of mammal communities increased with charcoal intensity. With reduction in species richness and increase in beta-diversity, the community organisation pattern in mammals can be termed as subtractive heterogenization (Socolar *et al.*, 2016). Therefore, even though mammal communities lost species at the local scale, their beta diversity, the spatial insurance is maintained. Conditional upon dispersability, the communities in future may undergo source-sink migration and mediate the local biodiversity loss (Leibold *et al.*, 2004).

For the beetle communities in our study area, we expected a pattern of subtractive biotic-homogenisation with disappearance of heterogeneous assemblages and

persistence of more tolerant species in response to charcoal intensity. However, we did not observe any significant pattern. This may be due to beetle communities being more resilient or high variability in arrangement of communities which produced the null effect (Azeria *et al.*, 2011; Ulrich *et al.*, 2012).

How does charcoal production structure communities?

The two significant community structuring patterns in response to charcoal intensity we observed in this study are subtractive homogenisation of trees and subtractive heterogenization of mammals. Following Segre *et al.*, (2014) and Chase *et al.*, (2011), these patterns can be attributed to two process of interspecific competition: deterministic exclusion and stochastic extinction. Deterministic exclusion imply an ordered non-random reduction of species richness which leads to homogenisation i.e. subtractive homogenisation. Stochastic extinction entails loss of species through random extinctions (thus, ordered by abundance) and increase in beta diversity(Segre *et al.*, 2014). Thus, assuming that the effect of hunting is equal across the gradient of charcoal intensity, charcoal production imposes dissimilar structuring mechanisms on different taxonomic groups.

Trees undergo biotic homogenisation due to deterministic exclusions, while mammals experience subtractive heterogenization due to stochastic extinctions.

Trees and mammals underpin two dominant ecosystem goods in the region: fuelwood (firewood and charcoal) and bushmeat. As the charcoal-preferred tree species decline, the ability of the woodland to provide charcoal decreases. At the same time, the other ecosystem goods and services derived from those species such as timber, firewood or medicine also reduce (Woollen *et al.*, 2016). The human communities in southern Africa, especially the poorest, use bushmeat from mammals in the woodlands as an important source of protein (Scholes *et al.*, 2004; MEA, 2005b). The decline in mammal populations and diversity due to charcoal production may reduce the availability and choices of bushmeat and affect the wellbeing of those people. In our study, the most commonly used species for

bushmeat – the common duiker – did not reduce in occupancy. However, the other favoured bushmeat species such as Springhare, Nyala and Aardvark reduced significantly, suggesting an overall reduction in opportunities for bushmeat acquisition.

Limitations of this study and future research

Being a space-for-time substation, this study is based on assumption that the difference in villages is due to charcoal production intensity. We could not repeat this study during the wet-season (2015) due to drought and civil unrest in Mozambique. This single dry season only provides an idea about the broad trends in ecological communities in response to charcoal production. However, further studies are needed to understand the charcoal production- biodiversity relationship in the region more effectively. We did not quantitatively asses the hunting patterns in the study region and therefore cannot quantify the effect of hunting (or lack of it). The sampling strategy for mammals did not represent the true occupancy as the sampling areas (500 m) were smaller than the dispersal ranges of many of the mammal species (e.g. African lion, African elephant and Side-striped jackal).

Multiple season and long term studies are required to validate our assumptions about the space-for-time substation. Our estimations could be improved by using more passive and accurate sampling methods such as camera traps and acoustic recorders. We did not include birds, reptiles and amphibians and other insects in this study. To obtain a general idea about biodiversity change these groups should be included. Therefore, for future, long term, multi-season assessments using multiple taxonomic groups is needed. Also, the role of beta-diversity should be empirically tested by monitoring the biodiversity of recovering-regenerating woodlands.

This study is based on species - level data and thus carries a potential for uncertainty associated with imprecise identification of some species. Further, since

it is a comparison between multiple taxonomic groups, there may be heterogeneity in species identification between these groups (Lewandowski et al., 2010). Identification-uncertainty in trees and mammals are more likely to be low than the relatively more cryptic group - ground beetles in this study and majority of the invertebrates (Driscoll, 2010). The species data of beetles in this study was based on the OTUs classified by the observed differences in morphological characters between the collected samples. This method may overlook the classifications based on subtle morphological differences and non-morphological characters within an OTU and hence underestimate the number of species (Foottit et al., 2009; Bozzuto et al., 2017). This underestimation may inflate the possibility of type II error in the beetle communities (Lewandowski et al., 2010). However, the possibility of missing species and underestimation of beetle diversity in this study is low, although not absent, as we compared the OTUs with the specimens in the natural history collection under the guidance of an expert. Nonetheless, the likelihood of such an error could be reduced by decreasing the taxonomic resolution and binning species into higher taxas - genus or family (Bozzuto et al., 2017). At the genus or family level, the morphological characters have relatively higher distinctness and thus identifications based on morphological characters are more consistent (Gaston et al., 1993). However, when the ratio of species: higher-taxa is high, more species per genus or family, it may obscure statistical detection of biodiversity patterns, especially biodiversity loss (Andersen, 1995; Bozzuto et al., 2017). The reliability and effectiveness of using higher taxa depend on species: genus ratio (Andersen, 1995). Quantification of this ratio, which varies between taxonomic groups and biomes (Lewandowski et al., 2010), is important before higher taxas can be used to investigate biodiversity change. Miombo being an understudied ecosystem, the method used in this study is thus more reliable than higher taxa based analysis which carries an additional caveat stemming from the ratio of species: higher taxas. Our inferences about beetle diversity are thus based on the assumption that OTUs are effective surrogates of beetle species.

Studies elsewhere have stressed upon the need to identify indicator taxonomic groups for assessment of biodiversity (Azevedo-Ramos et al., 2002; Schulze et al., 2004; Edwards et al., 2014). Other studies (Berry et al., 2010; Burivalova et al., 2014) have demonstrated the heterogeneity in responses of different taxonomic groups to land use. Since miombo is an understudied ecosystem in terms of biodiversity, understanding of patterns of biodiversity change across multiple taxonomic groups is more important than identification of an indicator group. In their multi-taxon comparison Edwards et al., (2014) noted that birds and beetles are effective indicators of biodiversity and demonstrated congruence among different taxonomic groups in beta diversity patterns. In the present study, we highlight that in context miombo, beetles may not be good indicators of biodiversity response. However, this study is a dry season spatial comparison and needs a multi-season perspective to validate and generalise this pattern. Further, among trees and mammals, we observed congruences in alpha diversity but divergence in beta diversity response. We here underline that response to land use may vary among taxonomic groups and land use activity. In context to the selective logging for charcoal production, tree communities may be more effective indicators of biodiversity change.

Further, birds are comparatively the most understood class of organisms (Bibby, 1999), are sensitive to habitat modifications (Owens et al., 2000) and are considered good indicators of biodiversity response to land use (Edwards et al., 2014) and effects of other habitat filtering process (Benítez-López et al., 2017). In this study, we did not include birds due to lack of expertise. Future studies in this area may expand our findings and compare the role of birds as indicators of impact of charcoal production on biodiversity.

Conclusions

This study concludes that charcoal production reduces alpha diversity across two of the three taxonomic groups we studied, but affects their beta diversities differently. It shows that charcoal production reduces the population size of the majority of

species. This study demonstrates that the turnover component of beta-diversity declines for tree communities and increases for mammals. In short, charcoal production is associated with subtractive homogenisation of trees and subtractive heterogenization of mammals.

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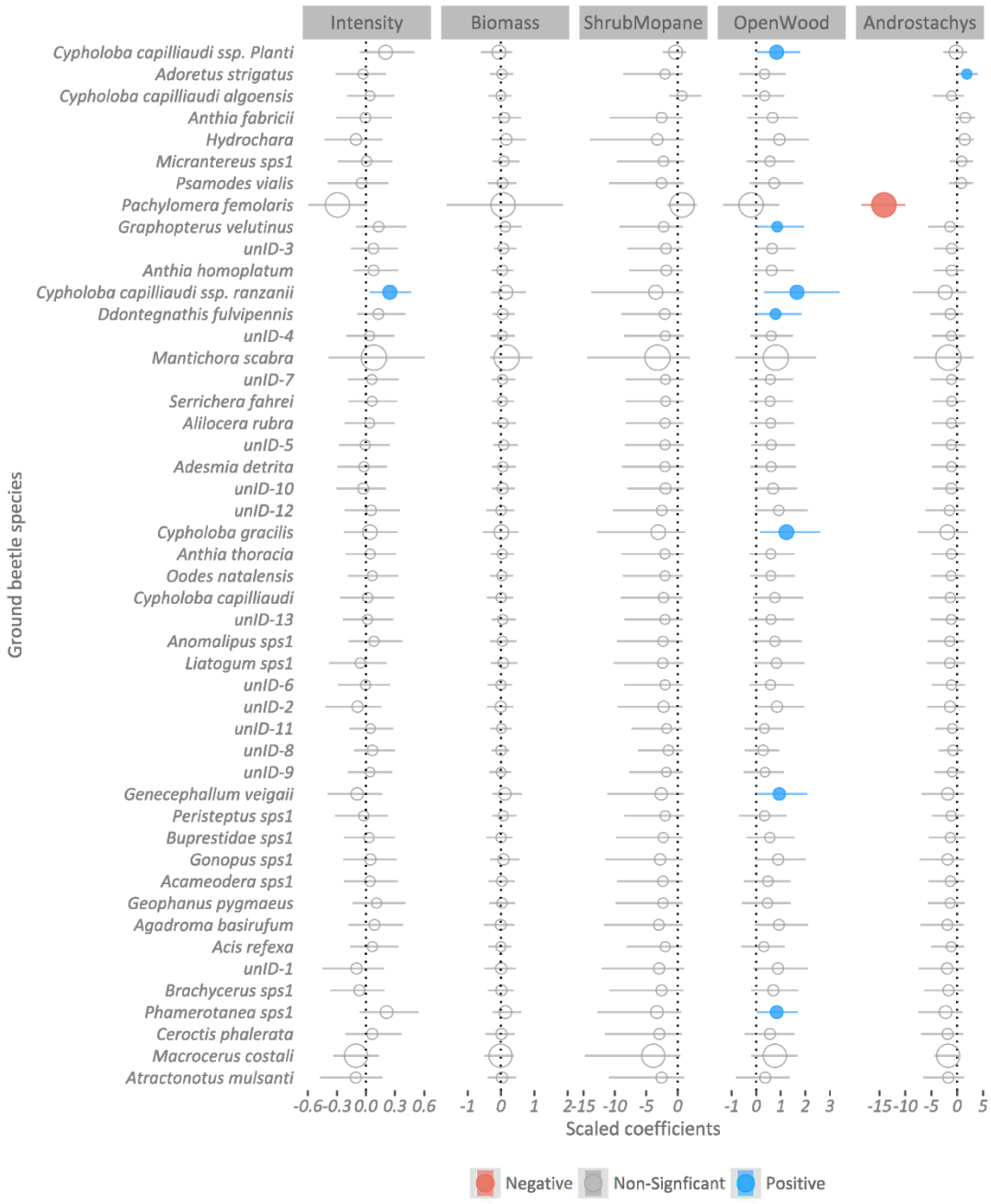
Supplementary material

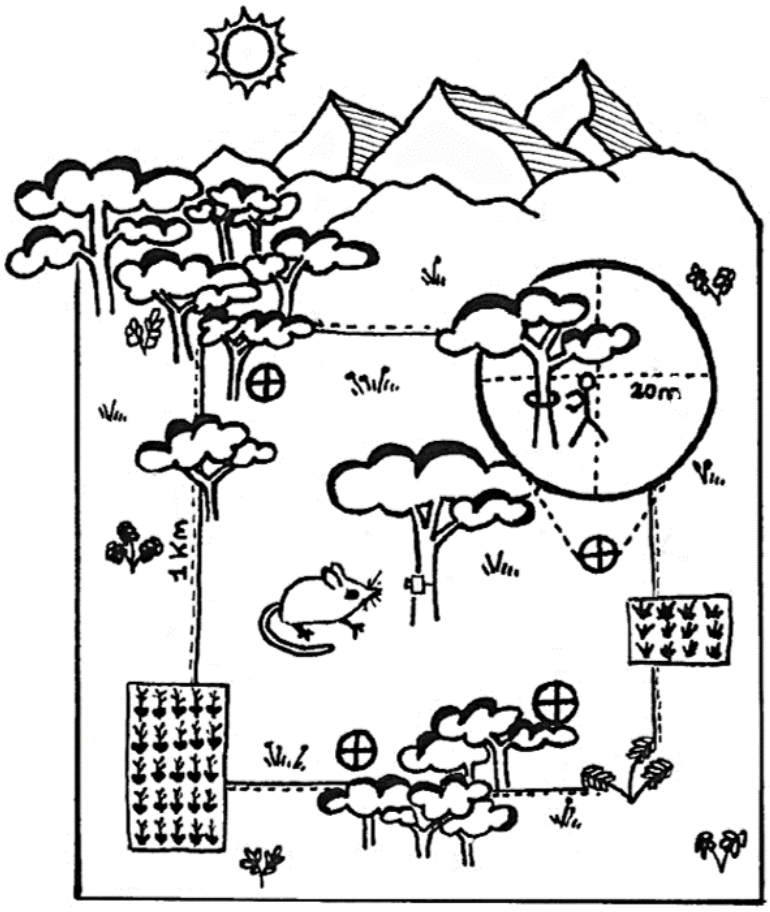


SM 1: Beta coefficients representing effects of intensity, biomass and landcover type on abundance of ground beetle species demonstrate the no effect of charcoal production intensity and woody-biomass on majority of species. Land cover had stronger effect on ground beetle communities compared to charcoal intensity. More species were significantly abundant in the open-woodlands. The positions of the circles represent scaled beta coefficients (per unit standard deviation), horizontal lines show 95% CI, colours indicate direction of the effect, and the sizes of circles denote the relative abundance of species.

Chapter 3

Agricultural expansion in the miombo woodlands of Africa – effects on tree and mammal communities

Hemant G. Tripathi, Casey M. Ryan, Emily Woollen



HGT conceived the research questions with inputs from CMR. HGT developed the study design with help from CMR. HGT collected the mammal data and performed the fragmentation analysis. EW collected the tree data. CMR prepared the biomass maps. HGT collated and analysed the data, and wrote the manuscript. CMR provided suggestions for analysis and comments on the manuscript.

Abstract

Aim: Agriculture is a leading cause of deforestation and habitat modification across the globe. It causes loss and fragmentation of habitats which influences biodiversity and intactness of ecological communities. Agriculture expansion in southern Africa is a dominant driver of deforestation in the miombo woodlands. How the agriculture expansion-led fragmentation and loss of woodland cover in the miombo woodlands affect biodiversity is poorly studied. The main aim of this study was to understand the patterns of organisation in ecological communities in response to fragmentation and habitat loss in the miombo woodlands.

Location: Miombo woodlands in the Gurue district of northern Mozambique

Methods: In this study, we used a single-season spatial comparison of chronosequence at 1km^2 scales. The chronosequence represented a gradient of fragmentation measured by the landcover division index (LDI). We sampled two taxonomic groups: Trees and mammal and examined their individual species-level and community-level responses to LDI, quantity of existing woodland-cover, and proportion of woodland-cover lost between 2007 and 2014. We used multiple measures of community-level response: species richness, turnover, and nestedness. To estimate the species and community-level parameters, we employed the single-season meta-community occurrence models which were analysed in the Bayesian framework.

Results: In response to LDI, trees and mammals showed the *more losers than winners* phenomenon. The abundance of 21 species of trees declined and only four increased with LDI. Mammal communities showed a non-linear response. At the lower levels of LDI, seven species increased in probability of occupancy and none declined. At the higher levels (~0.75) of LDI, two species significantly declined while none increased. At the community level, LDI was associated with linear declines in species richness of trees (-13.6%).

Species richness of mammal communities, however, increased (30.5%) at the intermediate levels of LDI (0.1-0.75) and declined (-15.5%) at the higher levels (0.75). Species richness of mammals also reduced (-25%) with the total woodland-cover. The turnover component of beta-diversity increased (4.5%) for tree-communities in response to LDI. Mammal communities increased in turnover (19.5%) in response to the woodland quantity.

Main conclusions: At the community level, species richness of trees decline linearly with fragmentation and woodland-cover loss. This indicates that trees follow a species-area relationship. As habitat shrinks, the number of tree species decline. Species richness of mammals, on the other hand, showed a non-linear relationship. It increased at the intermediate levels of fragmentation and declined when the fragmentation was above 75% and the habitat quantity was below 26.3%. In this study, thus, we show that not all taxonomic groups follow the fragmentation threshold hypothesis. With loss of species richness and increase in turnover, tree communities underwent subtractive heterogenization. Mammal communities, losing species at the higher levels of fragmentation, and beta-diversity with decreasing woodland habitat experienced subtractive homogenisation.

Keywords Africa, miombo woodland, savanna, agriculture expansion, fragmentation, habitat loss, taxonomic groups, trees, mammals, alpha-diversity, beta-diversity, occupancy, Bayesian, Mozambique.

Introduction

Loss and fragmentation of natural habitats reduces biodiversity (Andrén, 1994; Fahrig, 2002, 2003a; Cordeiro *et al.*, 2015; Hanski, 2015) and disturbs the intactness of ecological assemblages (Jamoneau *et al.*, 2012; Püttker *et al.*, 2015), with consequences for the functioning and resilience of ecosystems (Didham *et al.*, 1996). In the miombo ecoregion of Africa, agriculture is a leading cause of habitat modification, but its implications on biodiversity is understudied. Here, we investigated the effects of fragmentation and habitat loss caused by agricultural land use and their impact on diversity and composition of trees and mammals in the miombo woodlands of northern Mozambique.

Human activities have extensively modified the Earth's surface (Ramankutty *et al.*, 2008; Ellis, 2011) and altered the structure of ecosystems, reducing their biodiversity, functioning, resilience, and ability to provide ecosystem services (Hooper *et al.*, 2012; Barnes, 2015; Oliver *et al.*, 2015). Agriculture is crucial for food security, livelihoods and wellbeing of people, and is a dominant land use activity and a primary cause of deforestation in tropical ecosystems (Leblois et al. 2017; DeFries et al. 2010; Ramankutty et al. 2008; Ramankutty & Foley 1998). Deforestation alters ecological communities through landscape processes: habitat loss and fragmentation (Dunning *et al.*, 1992; Geist *et al.*, 2002; Bogaert *et al.*, 2011), which reduces biodiversity (Hanski, 2015). Agricultural production, therefore, is also a major driver of the ongoing biodiversity crisis (Tscharntke *et al.*, 2005; Newbold *et al.*, 2015).

The biodiversity of the miombo woodlands, a dominant socio-ecological savanna ecosystem in southern Africa (Frost, 1996), is globally significant due its high endemicity of species (Mittermeier *et al.*, 2003; Linder *et al.*, 2012). Furthermore, it is socially important because local communities, especially the poorest, derive essential ecosystem services and wellbeing from it (Scholes *et al.*, 2004; Ryan *et al.*, 2016). Yet the miombo ecoregion is poorly described and little understood in terms

of how it responds to land use and land cover change (Murphy *et al.*, 2016). In the miombo region, and also most parts of Africa, small-scale subsistence or commercial farming is a widely practised form of agriculture, while export-driven commercial farming is expanding (Leblois et al. 2017; Fisher 2010; DeFries et al. 2010; Ryan et al. 2014). Small-scale farming involves clearing of woodland areas to create small agricultural fields (1.74 ± 0.51 ha, Ryan et al. 2014), causing small-scale deforestation (Ryan *et al.*, 2012) that results in a heterogeneous agro-ecological landscape consisting of a mosaic of fields, fallows and woodland patches (Kamusoko *et al.*, 2007; Ojoyi *et al.*, 2016). The quantity and continuity of habitats are determined by the degree of habitat loss and fragmentation respectively (Jaeger, 2000; Bennet *et al.*, 2010), but this heterogonous matrix of anthropogenic and natural land covers (an 'agro-ecosystem') may support higher levels of biodiversity than the natural landscapes through reciprocal socioecological relationships (Dorresteijn *et al.*, 2015), and provide a range of ecosystem services (Sileshi *et al.*, 2007; Decocq *et al.*, 2016).

In addition, being a historically human-managed semi-natural system (Ellis *et al.*, 2010), which has co-evolved with the land-use activities of people and is characterised by frequent disturbances (Stromgaard, 1985; Ryan *et al.*, 2011), the miombo woodlands may be more resilient to the intermediate land-use changes (Kalaba *et al.*, 2013; McNicol *et al.*, 2015) compared to other tropical biomes. However, the rapid expansion of agriculture to meet the needs of the growing human population, and to some extent also that of the commercial markets (Fisher, 2010), is now leading to extensive deforestation (Ryan *et al.*, 2014; Schneibel *et al.*, 2016) and drastic shifts in the structure, quantity, and distribution of woodland habitats in this socio-ecological system. With relatively large areas of woodland suitable for cultivation still remaining, agricultural expansion is a main source of economic development in this region, often at the expense of woodland cover (Leblois et al. 2017). The growing demand for agricultural products, improved infrastructure and technology, along with the introduction of commercial crops, will

more likely increase access and provide incentives to expand agriculture in to new frontiers. Agricultural expansion for local needs, coupled with commercial farming, therefore, may convert even the last remaining habitats, change the traditional intermediate landscape to a more production oriented agriculture dominated landscape, and cause extensive losses and fragmentation of the woodland habitat, which may have severe consequences on biodiversity and the ecosystem services underpinning it (Searchinger *et al.*, 2015).

How ecological communities respond to habitat loss and fragmentation in the miombo woodlands is largely unknown, but studies elsewhere show that intermediate levels of fragmentation and habitat loss may create land cover heterogeneity leading to greater resource and niche diversity, reduced species competition, and persistence via resource complementation and supplementation, existence of multi-predator systems, and a consequent increase in the landscape-wide species pool (Dunning *et al.*, 1992; Andrén, 1994; Pardini *et al.*, 2010; Eycott *et al.*, 2011; Tscharntke *et al.*, 2012; Magrach *et al.*, 2014b; Magioli *et al.*, 2015). The semi-natural systems with traditional small-scale agriculture, therefore, maintain significant biodiversity at the landscape level (Fischer *et al.*, 2012; Dorresteijn *et al.*, 2015). The miombo-agriculture mosaics likewise are known to retain biodiversity, especially of trees and mammals: trees consisting of woodland species in addition to the useful fruit-fodder-timber species (Frost, 1996; Sileshi *et al.*, 2007) and mammal communities mainly comprising medium to small sized species (Linzey *et al.*, 1997; Caro, 2001). However, when agricultural land cover expands, the quantity and size of natural habitats reduce as they become increasingly fragmented in the agriculture dominated matrix (Bennet *et al.*, 2010).

Fragmentation, in tandem with habitat loss, is known to modify ecological processes and restructure communities, typically resulting in reductions in species populations and causing local extinctions (Bogaert *et al.*, 2011; Hanski, 2015). The adverse effects of fragmentation are linked to alterations in landscape-scale physical and biotic processes (Ewers *et al.*, 2006). As habitat patches across the landscape

become more fragmented, the length of edges increase, imposing pronounced 'edge effects' on the ecological communities (Watson *et al.*, 2004; Broadbent *et al.*, 2008; Magrach *et al.*, 2014a). Increases in the length and density of edges create abrupt artificial boundaries that intensify predation, herbivory and exploitation by humans via hunting and harvesting (Rathcke *et al.*, 1993; Magrach *et al.*, 2014a). In addition, with fragmentation, the habitats condense, increasing inter- and intraspecific competition for food, forage and habitat space, and also become more isolated, which impairs migration and colonization, thereby resulting in decreases in population densities (Andrén, 1994; Fahrig, 2002; Russildi *et al.*, 2016). These processes can push certain species – particularly habitat specialists – to extinction, and release others – mostly the generalist, fast-growing/reproducing or other resilient species – from extinction pressures (Hill *et al.*, 1999; Jamoneau *et al.*, 2012). However, the effects of fragmentation are not always linear. At the intermediate level, the habitat (the woodland patches) and the intervening matrix (the non-woodland patches) together create a heterogeneous mosaic. This mosaic is often associated with positive effects on species populations due to the niche diversity and complementarity in resources from different fragments which relaxes competition pressures (Conde y Vera *et al.*, 2006). But at higher levels of fragmentation, the habitat patches become more isolated, restricting species' ability to forage and make use of multiple habitat patches, which leads to their decline (Andrén, 1994; Ewers *et al.*, 2006; Bennet *et al.*, 2010). Thus, fragmentation and reduction in habitat quantity generally cause biodiversity loss and changes in composition of the landscape-wide species pool (Tscharntke *et al.*, 2012).

To mitigate biodiversity loss, a number of management strategies have been proposed, such as increasing the area under protection (CBD, 2010) by extending its coverage to agricultural lands and maintaining biodiversity within the agricultural landscape via land-sparing or sharing, or both (Fischer *et al.*, 2008; Balmford *et al.*, 2012). Thus, there is a clear impetus to reconcile agricultural land use with biodiversity conservation since agriculture – which is already a dominant landcover

representing nearly one-third of terrestrial land surface – is projected to expand with growing demands for agricultural products in the future (Scherr *et al.*, 2008; Ellis *et al.*, 2010; Clough *et al.*, 2011; Laurance *et al.*, 2014). However, to integrate production agriculture and conservation of biodiversity, a thorough understanding of their inter-relationships and the key drivers that facilitate biodiversity in these landscapes is imperative (Benton *et al.*, 2003; Sayer *et al.*, 2013). Understanding the effects of the twin landscape processes of habitat loss and fragmentation on the organisation of ecological communities, therefore, can be an important tool to not only assess but also to predict the impact of agricultural land use on biodiversity at the landscape scale, and thereby inform land management policies and practices (Fahrig *et al.*, 2011). For example, in the soya-dominated deforestation frontier in the southern Amazon, Macedo et al. (2012) highlighted the effectiveness of efficient use of previously cleared land and showed that increased production and forest conservation by land sparing can coexist. But how much land should be spared or forest be conserved to contain biodiversity in the agricultural landscapes, what kind of biodiversity should be conserved, and what the associated trade-offs with agricultural production might be, are all unknown. Thorough knowledge of landscape-level thresholds of habitat loss and fragmentation, as well as the tipping points of biodiversity at species- and community-level, will help determine the required spatial structure and the desired ecological communities for sustainable biodiversity management. In the context of the Miombo region, with commercial farming still at a nascent stage, with human population densities low, and biodiversity and habitats, although disturbed, relatively intact (Mittermeier *et al.*, 2003), there is scope to design and streamline agricultural policies to improve biodiversity conservation and ecosystem service management within the changing agricultural system.

We carried out the present study with the objectives of understanding the effects of agriculture-driven landscape processes – fragmentation, remaining habitat quantity and habitat loss – on ecological communities in the understudied and dynamic

miombo woodlands, explore the miombo-specific context to the global biodiversity-agricultural land use paradigm, and identify locally relevant thresholds of habitat loss and fragmentation. Since biodiversity response can be multi-faceted and vary between taxonomic groups, we examined biodiversity of mammal and tree groups, as they are commonly used to supply ecosystem services and wellbeing (Frost, 1996; Sileshi *et al.*, 2007; Ryan *et al.*, 2016), and are suitable for studies at multiple levels (community: alpha and beta, and species). We present a multi-taxa, assemblage-level assessment of biodiversity response to agriculture land use in the miombo woodlands of northern Mozambique at landscape (1 km^2) scales.

Specifically we investigated the following questions:

(a) Species response: Which species increase or decrease in occurrence ('winners' and 'losers') in response to fragmentation and loss of woodland cover?

(b) Community response: How does alpha (species richness) and beta diversity (species composition) change in response to fragmentation, quantity and loss of woodland cover?

(c) What are the thresholds of fragmentation and habitat quantity above which biodiversity begins to decline in miombo woodlands?

Methods

Approach

We used 'space-for-time' substitution in this study, having assumed that spatial variation in the ecological communities that we studied are results of their respective temporal land-use and land-cover change histories. For each community of each taxonomic group, we collected occurrence data (counts for trees and incidence for mammals). We analysed multi-species occurrence using hierarchical meta-community models (Dorazio *et al.*, 2005) in a Bayesian framework, using Markov Chain Monte Carlo (MCMC) simulation.

Study area

We carried out this study in Posto Administrativo (PA) Lioma, in the district of Gurué, located in the northern part of Zambézia, the second most populous province in Mozambique (Figure 1). Small-scale agriculture is a dominant land use in Zambézia, representing more than 20 % of small-scale farmers in the country (INE, 2014). In addition, commercial farming is rapidly developing, making Zambezia one of the main soya-producing frontiers in Mozambique (Hanlon *et al.*, 2012). Lioma, with a population density of 64.3 inhabitants/km^2 is one of the most densely populated regions in the province (INE, 2014). The humid climate, with precipitation of 1030 mm year^{-1}, and seasonal rainfall from November to April, is suitable for agriculture (INE, 2014). People mainly cultivate subsistence crops like maize, cassava, rice and beans, and important cash crops like pigeon pea, soya, cowpea, sunflower and sesame(INE, 2014). Small farms of 1.5-2.5 ha in size cover about 90 % of the agricultural land in the region(Hanlon *et al.*, 2012). The commercial farming for soya, which was first introduced in the 1980s by Brazilian companies, stopped due to the civil war (1977-92), and was reinstated in 2002 Matteo *et al.*, 2016). Since then, commercial farming – mainly driven by the national demand for soya – has been steadily growing in the region, now equalling 2.8 % of

agricultural land and contributing to about 35% of the soya production(Matteo *et al.*, 2016).

Due to the increasing demand of soya, large-scale companies have started to invest in soya production, making commercial farming a major driver of land use change(Matteo *et al.*, 2016, Baumert *et al.*, 2017 - in prep). The expansions of subsistence farming and the introduction of market-driven commercial agriculture are the main causes of deforestation – and thereby loss and fragmentation of woodland cover – in this landscape.

Fragmentation and woodland cover in the region

Fragmentation analysis here uses intact miombo woodland as a reference. To identify the miombo woodland and asses changes in its cover, we made above-ground woody-biomass maps for 2007 and 2014 using images obtained by the Phased Array L-band Synthetic Aperture Radar sensor on the Advanced Land Observing Satellite (ALOS PALSAR), following the methods described in Ryan et al. (2012). We classified all pixels above the threshold of 15 tC ha^{-1} as woodland, and all pixels below this value as non-woodland. We divided the study area into 1 km^2 grids, each square of which would represent a landscape-scale sampling unit (LSU). To ensure that the grids are representative of miombo landcover, we excluded the grids with mean elevation of 800m above sea level (ASL) and above, as miombo woodlands are known to decrease from about 1000m ASL (Shirima *et al.*, 2011). The following landscape-level processes were analysed at 1km^2 scale: (i) fragmentation: measure of discontinuity in woodland cover, (ii) habitat quantity: the amount of remaining woodland cover in 2014, and (iii) habitat loss: amount of woodland cover lost between 2007 and 2014. Habitat quantity and habitat loss in most cases are correlated, but a landscape can naturally have lower habitat quantities without undergoing habitat loss, so the latter was included to take in to account this inherent variation.

Using the Landscape ecology Statistics (LeCos) tool developed by Jung (2012), and the *Python* package NLMpy by Etherington et al. (2015), we evaluated fragmentation (i), habitat quantity (ii) and habitat loss (iii) as:

(i) Landcover Division Index (LDI): Indicator of the degree of habitat coherence; defined as the probability that two randomly selected points in the landscape are situated in two different patches of the habitat (Jaeger, 2000; Mcgarigal, 2015)

(ii) Total woodland cover (TWC): Proportion of the 1 km grid occupied by woodland cover.

(iii) Proportion of decline in woodland cover (WC-loss) between 2007 and 2014.

We used LDI as an indicator of fragmentation and the proportion of TWC and its loss (WC-loss) as a measures of habitat quantity and habitat loss respectively as they are intuitive and relatively easily understood metrics in context to land management.

A number of fragmentation metrics (or indices) such as number of patches, nearest neighbour distance, splitting index, fractal index, effective mesh size, splitting index, etc. have been proposed and used in several studies (Hill *et al.*, 1999; Jaeger, 2000; Magrach *et al.*, 2014b; MacLean *et al.*, 2015). However, these metrics often describe similar processes, are inter-related and often are partially or wholly redundant inherently or empirically (Mcgarigal, 2015). We used the proportion of woodland instead of mean patch size as it is a more direct way of representing quantity of habitat present in the landscape. Jaeger (2000), after comparing various indices of fragmentation, concluded that effective mesh size (EMS) was most suitable for comparing fragmentation among landscapes with varying habitat quantities. However, in the landscapes we studied, EMS was highly correlated with LDI (R^2=0.86 for mammal grids, R^2=0.83 for tree grids). We used LDI because its simplicity should make it more intuitive. LDI was also correlated with TWC

(R^2=0.77), but we used both in order to assess their independent effects, and to identify thresholds for both. As TWC and WC-loss were correlated with LDI, we used the residuals (i.e. the amount of variation not explained by LDI) of their relationships with LDI. Hereafter, 'TWC' and 'WC-loss' refer to residuals of TWC~LDI and WC-loss~LDI, respectively.

Diversity data collection

We collected species-level occurrence data for each LSU: abundance for trees using 20 m radius circular plots, and incidence for mammals using camera traps (Figure 1). For this study, we used the tree data post-hoc by identifying all the circular plots falling within the LSUs and choosing grids which had 2-4 tree plots, finally selecting 39 grids containing a total of 96 tree plots. Within each tree plot, the diameter at breast height (DBH) of all tree stems above 5 cm DBH was measured, and the stems were identified by their local names, with the help of local experts. Any stems unidentified in the field were collected and identified later by reference to field guide (Palgrave *et al.*, 2002; these were also used to assign scientific names to all stems). The tree identification was further cross-validated by botanists at the University of Eduardo Mondlane in Maputo. The trees that could not be identified (n=13) were considered as distinct unknown species and given unique codes.

To sample mammal communities, we selected 40 LSUs representing a gradient of fragmentation from low to high, by dividing all the grids in the landscape in to 10 classes of LDI (0.1 to 0.9) then randomly selecting 4 grids from each class. Within each LSU, we placed one camera trap within 100 m of the centre, at the best camera trapping location, chosen as an open and frequently used pathway, to maximize detection of species (O'Connell et al. 2011). The cameras were visited every week to download the images and check their functioning. Each LSU was considered as a site and every day-night period of the camera trap a sampling occasion. The sampling occasions provided detection information for each species: 0 for no detection and 1 for detection. Camera traps were supposed to be operated for about

60-65 days, however, due to camera thefts (n=3; excluded from the analysis), disturbance by people, and inclement weather conditions, not all cameras recorded an equal number of camera-days. The camera-days ranged from 8 to 65 and had a mean of 45 days. Mammals in camera-trap images were identified to the species level where possible, by reference to field guides (Liebenberg, 2000; Kingdon, 2001; Stuart *et al.*, 2007; Gutteridge *et al.*, 2013). Where species identification could not be made (n=5), the morphologically distinct individuals were classified to the lowest possible taxonomic group (genus, family or order) and given unique identification codes.

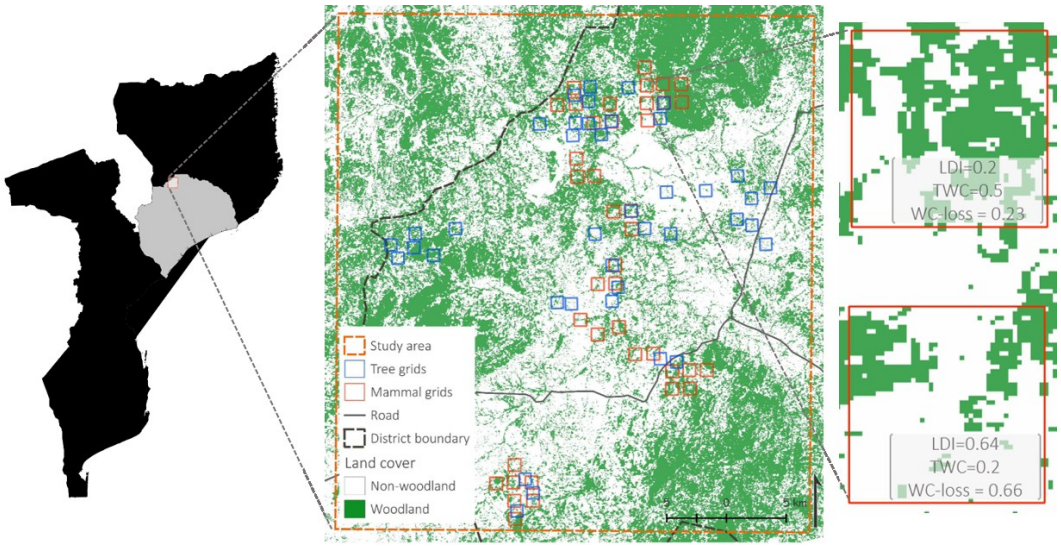


Figure 1: The study area in Zambézia province in north central Mozambique. We identified several landscape sampling units (1 km² grids) within which we collected incidence data of mammal (red boxes) and count data of tree species (blue boxes) and also computed the land cover variables: Land division index (LDI), total woodland cover (TWC) and woodland cover loss between 2007 and 2014 (WC-loss).

The tree plots and camera traps were located in different LSUs because they were sampled as part of different studies. For trees, the plot sampling and LSU selection were done before the fragmentation analysis. For mammals, on the other hand, sampling and LSU selection was done after fragmentation and represented a stratified gradient of fragmentation from low (0.1) to high (0.9). The LSUs of trees and mammals are comparable through their predictor variables – LDI, TWC, and WC-loss.

Data analysis

To estimate the total species richness (meta-community state) and accumulation, and to assess survey completeness, we used the Hill number and sample-based rarefaction and extrapolation (Chao *et al.*, 2014; Hsieh *et al.*, 2016).

Further, using the species data that we collected, we derived two types of parameters: (i) the species state: abundance or occupancy of species, an indicator of individual species response, and (ii) community state: species richness (alpha diversity) and species composition (beta diversity), indicators of the community level response. We identified appropriate models for each of the state variables and investigated the possible relationships between the state variables and the landcover variables: LDI, TWC and WC-loss, using the following model frameworks:

Species state

The abundance of tree species was modelled as a Poisson process. The state of mammal species was observed as incidence from the camera trap surveys and therefore modelled as a Bernoulli process.

For trees, we assumed that all tree species have equal and perfect probability of detection. We therefore included the occurrence data of trees without any replication, but we still modelled the LSU-level variation in abundance per tree species. We modelled tree counts using a Binomial (detection part)-Poisson (count) regression model adapting the Dorazio/Royle/Yamaura (DRY) model (Yamaura *et al.*, 2012).

To estimate occupancy of mammal species we used the Dorazio/Royle (DR) community occupancy model (Dorazio *et al.*, 2005, 2006) where we took into account heterogeneity in detection by undertaking temporally replicated camera trap surveys within each camera trap grid.

For both taxonomic groups, to account for dependence between species, we treated species-specific effects as random by drawing them from a common distribution. We relied on the assumption that species-specific effects are stochastic and exchangeable – "*similar although not identical*" (Kéry *et al.*, 2012, 2016). Therefore, the models that we employed for analysis of species occurrence are effectively multilevel mixed-effects hierarchical models.

Community state

From the output of the species-state models, we computed two community-state parameters: (i) species richness (SR), and (ii) mean community dissimilarity (MCD) – a measure of variation in community composition, or beta-diversity. The MCD is equivalent to the Local Contribution to beta Diversity (LCBD) of Legendre & De Cáceres (2013). Communities can change in species composition due to two processes: (i) replacement of species and thereby turnover in the community, and (ii) loss of species with low or no turnover and thereby nestedness in the community. We computed both the turnover and the nestedness components of the multi-part Sorenson dissimilarity, after Baselga (2010).

The community state parameters were estimated as posterior means within the community occurrence model framework (N-mixture for trees and occupancy for mammals), using the detection-corrected matrix of species occurrence. The community estimates derived from the posterior distribution are not independent, as they are based upon two related estimates – the mean and standard deviation of the estimated mean. We modelled the posterior mean estimates using a simple regression, and propagated the estimation uncertainty (i.e. the standard deviation) by constructing two residual components. The first component is the known uncertainty based on the posterior standard deviation of the estimate, and second residual component is the lack of fit from the simple regression model. Hereafter we refer to the models for explaining the community state parameters as 'community-state models'.

Model analysis and inference

We analysed the above-mentioned models using a Bayesian approach. We chose Bayesian analysis because fitting the meta-community model (which makes inferences at the three hierarchical levels – meta-community, local community and species in the same framework) is more easily done in Bayesian than frequentist approaches (Kéry *et al.*, 2016). Complex models like the ones used here – community level-multispecies models with detection and occupancy parameters and species treated as random effects – are easier to fit and write in the BUGS language. Model description in the BUGS language and algebra is identical, flexible and intuitive. Further, Bayesian framework provides precise measures of uncertainty in parameter estimates as it uses probability to make statements about the unobserved quantities which are treated as random variables(Kéry *et al.*, 2016). Whereas, the frequentist paradigm which uses repeated samples is based asymptote (maximum likelihood) and does not make direct probability statements. Instead it makes inference about the probability of getting the observed data (Kéry *et al.*, 2016).

We specified the models in BUGS language and executed simulations using 3 Markov chains, with 75, 000 iterations for each chain (the first 25,000 iterations of which were discarded as burn-in), and set the thinning rate to 50, yielding 3,000 samples from the posterior distributions.

Our objective in this study was to test relationships between response (species and community state) and landcover variables (i.e. LDI, TWC and WC-loss), so we built the species and community models with landcover variables as predictors in additive combination (Table 7). Since the effects of fragmentation can be non-linear (Andrén, 1994; Fahrig, 2002, 2003b; Ewers *et al.*, 2006), we also included the cubic term of LDI, compared the models with and without the cubic term, and selected the ones with lower deviance and predictive error. In total, we constructed two sets of two occurrence models: one each for trees and mammals, and three community-state models (alpha, beta-turnover and beta-nestedness) for each group. We checked all the models for convergence using the Gelman-Rubin convergence diagnostic,

with potential scale reduction factor (PSRF) values approaching 1 (and no higher than 1.1) considered acceptable (Gelman *et al.*, 1992). We used the 95 % Bayesian Credible Interval (CI) to indicate significant effects; if the bounds of the 95% CI did not contain zero, the effect was considered significant (Kéry *et al.*, 2016).

Summary of models

(a) Species state

Table 1: Details of the hierarchical occurrence models accounting for detection for the trees and mammals

Taxonomic group:	Trees	Mammals
State process: occurrence	N_{ik} ~ Poisson (λ_k)	z_{ik} ~ Bernoulli (Ψ_k)
Observation process: detection	$Y_{ik} \mid N_{ik}$ ~ Binomial (N_{ik}, p_{ik})	$Ysum_{ik} \mid z_{ik}$ ~ Binomial (J_i, $z_{ik}p_k$)
Models of species heterogeneity in occurrence	log (λ_{ik})= $\beta 0_k$ + $\beta 1_k$ * LDI + $\beta 2_k$ *TWC+ $\beta 3_k$ * WC-loss	logit (Ψ_{ik})= $\beta 0_k$ + β_k * LDI + $\beta 2_k$ *LDI^3 + $\beta 3_k$ * TWC + $\beta 4_k$ * WC-loss
Detection heterogeneity	logit (p_{ik})=$\alpha 0_k$	logit (p_{ijk})=$\alpha 0_k$

The unobserved latent states of species *k* at site *i* for tree count (N_{ik}) and mammal incidence (z_{ik}) were modelled as a Poisson distribution with expected abundance (λ_k), and Bernoulli trial with expected probability of occupancy (Ψ_k), respectively. The observed data for tree counts (Y) and total number of mammal incidences (Ysum) were both simulated as Binomial trials with a probability which is the product of the species occurrence and detection probability (p_k).

The occurrence probability for trees (λ_k) and mammals (Ψ_k) was modelled by the following predictors: (i) LDI in linear and (ii) cubic term (LDI3); (iii) proportion of woodland cover (TWC), and (iv) proportion of woodland cover loss (WC-loss) in additive combination with $\beta 1$, $\beta 2$, $\beta 3$ and $\beta 4$ as their beta coefficients respectively and $\beta 0$ as intercept. The detection probability of trees comes from the variation between sites, as tree data are not replicated, since we assumed homogeneity within

the site. We did not model detection probability and thus the model for detection probability contains only the intercept ($\alpha 0$). For both, detection and occurrence, the species-specific parameters (indexed by k) were constrained and drawn from a common normal prior distribution.

So, $\boldsymbol{\beta_k \sim Normal\ (\mu_\beta\ \sigma^2_\beta)}$, $\boldsymbol{\alpha_k \sim Normal\ (\mu_\alpha\ \sigma^2_\alpha)}$.

(b) Community state

The community states of species richness and beta diversity (the latter with its turnover and nestedness components) were computed on the detection-corrected estimates of true species occurrence. They had two interrelated estimates: the posterior mean and standard deviation. We model the c^{th} community parameter at site i, A_{ic} as a normal distribution with estimated mean (μ_{ic}) and its known standard deviation (σ^2_{ic}). We then used the mean (μ_{ic}) of this distribution in a regression model as response variable for predictors in additive combination and with residual error, $\boldsymbol{\varepsilon_c}$.

$$\boldsymbol{A_{ic} \sim Normal\ (\mu_{ic}\ \sigma^2_{ic})}$$

$$\boldsymbol{\mu_{ic} = \beta 0_c + \beta_c * Intensity_i + \beta 2_c * landcover_i + \beta 3_c * biomass + \varepsilon_c}$$

R packages and functions

We computed the sample-based total species richness, accumulation and survey completeness using the *iNEXT* package (Hsieh *et al.*, 2016). We used the *adespatial* package to calculate the turnover and nestedness components of beta diversity. To fit the Bayesian models specified in BUGS language we used the *jagsUI* package (Kellner, 2015). For constructing the meta-community models in R framework, we used the R-codes in Kéry & Royle (2016) and Kéry & Schaub (2012). Figures were drawn using *ggplot2* (Wickham, 2009).

Results

Survey effort, meta-community size and commonly occurring species in the region

We measured a total 3770 stems of trees and encountered 986 incidents of mammals (from 1693 trap nights) belonging to 88 and 21 species, respectively. Both taxonomic groups reached an asymptote in species accumulation and attained significant survey completeness (SC = >95 %) (Figure 2). The extrapolated sample-based estimation of meta-community size (i.e. total number of species in the study area without accounting for detection heterogeneity) was lower than the detection-
10 corrected estimate from the hierarchical model (Table 2). This means that without accounting detection, the sample based species accumulation is underestimated.

Based on the models, at the meta-community level, the tree communities may contain about 140 species, while mammal communities may have about 34 species.

Table 2: Summaries of species estimation for the two taxonomic groups - trees and mammals at meta-community (gamma diversity) and community level (alpha diversity)

	Trees		Mammals	
	mean (n=96)	95% CI	mean (n=37)	95% CI
Community size: plot-level mean species richness	6	5.8 - 6.1	4	3.8 - 4.2
Difference between communities - Beta diversity	82.05	81.94 - 82.17	17	16.8 - 17.2
Meta-community size - observed total species richness	88		21	
Sample based estimate of total species richness	114.2	97.42- 160	21.9	21.1 - 29.2
Model-based detection-corrected estimate of total species richness	140.4	124 – 150	33.5	22 - 49
Sample completeness	0.96		0.98	

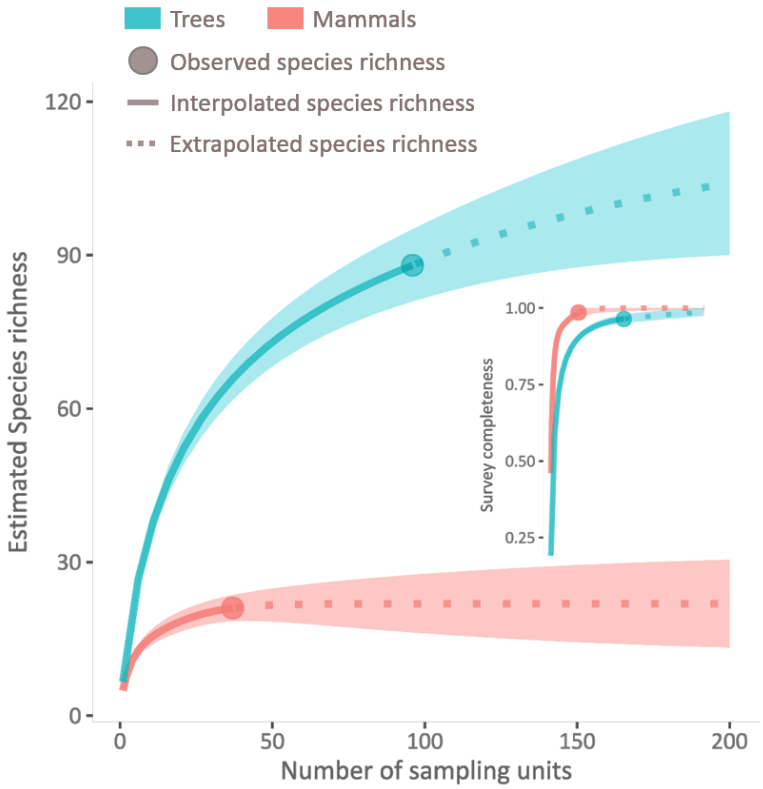


Figure 2: The sample rarefaction- and extrapolation-based species richness estimate and accumulation curve with 95% confidence interval (the shaded region) shows species asymptote and survey completeness (>0.97), indicating that our study covered most of the species found in the region for both taxonomic groups (trees and mammals). The detection-corrected species richness estimates from the hierarchical models were higher than the above-shown sample-based estimates.

Among the tree species across the study region, *Combretum collinum* mainly occurred in areas with high fragmentation and woodland loss, and was the most abundant species in the region (Figure 4). Species of genera *Brachystegia*, a key genera of the miombo woodlands, primarily occurred in areas with more continuous and high woodland cover. *Brachystegia boehmii* and *Julbernardia globiflora* were the key miombo species among the top 12 abundant tree species in the region which represented ~50% of all trees.

For mammals, we estimated the probability of occupancy across the study area while accounting for detection heterogeneity between species. The estimated community-level mean occupancy (Ψ_{μ}) of mammals in the region 0.24 (SD±0.27),

while the species-level occupancy (Ψ) ranged from 0.047 to 0.93, indicating high variability between species. The species detection (p) ranged from 0.01 to 0.28, with community mean detection (p_{μ}) at 0.054 (SD±0.9) (Figure 3).

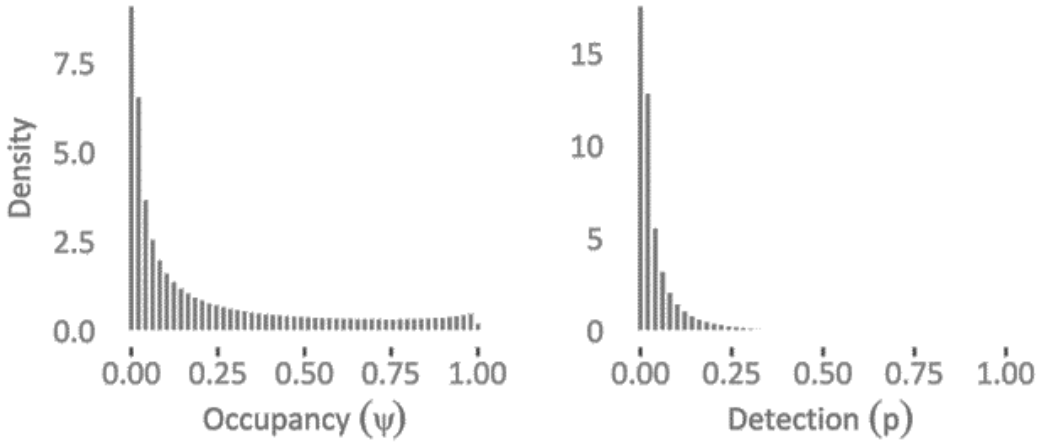


Figure 3: Distribution of community level average occupancy (Ψ_{μ}) and detection probability (p_{μ}) between mammal species based on parameters from the hierarchical occurrence model (Ψ_{μ}, $\Psi\sigma^2$, p_{μ}, p_{σ^2}) for the scale of 1 km² and single season survey (April-July) in 2016.

Of the 21 species of mammals we encountered, the most commonly occurring species during our study was the elephant shrew (*Elephantulus sp.*) followed by murids such as thicket rat (*Grammomys* sp.), African spiny mouse (*Acomys* sp.) and African giant rat (*Cricetomys gambianus*) and other species such as rock hare (*Pronolagus rupestris*). The slender mongoose (*Galerella sanguinea*) and rusty-spotted genet (*Genetta maculata*), along with the domestic cat (*Felis catus*), were the most commonly occurring predators in the region (Figure 5). All of the murids, the elephant shrew, the rock hare and the common duiker (*Sylvicapra grimmia*) are commonly hunted using dogs, though many other species are likely to be consumed if caught (personal observation and Timberlake et al. 2009).

Figure 4: Tree species found in the study area ordered by abundance, indicating dominance of non-miombo species in the region. The top 12 most abundant species account for over 50% of all trees observed during the study. Brachystegia boehmii and Julbernardia globiflora are representative of miombo in the top 12 species.

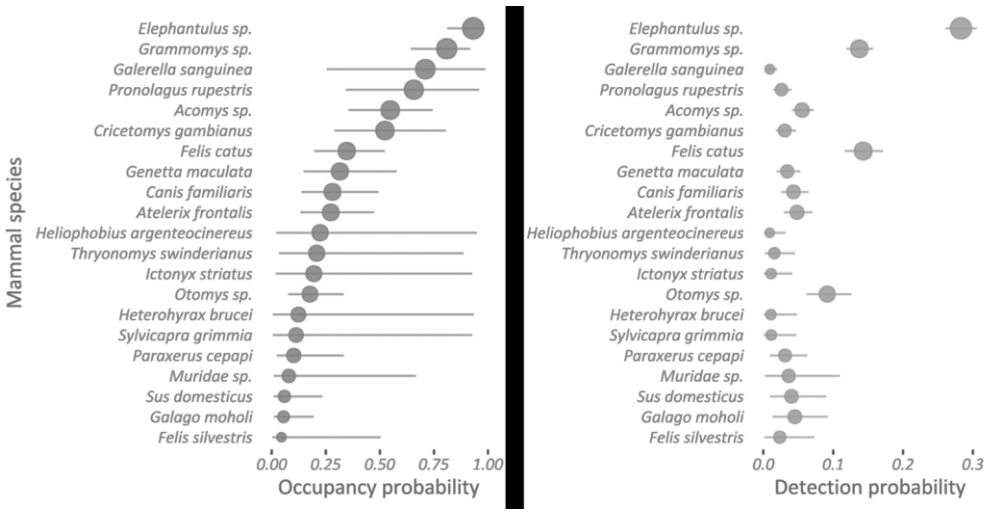


Figure 5: Occupancy and detection probabilities of mammal species at the scale of 1 km² during early dry season (April-July) 2016. The mammal communities in the miombo-agricultural landscape are dominated by the elephant shrew (Elephantulus sp), murids (such as Grammomys sp. and Acomys sp.) and the rock hare (Pronolagus rupestris). Mongooses (Galerella sanguinea) and genets (Genetta maculata) are the dominant predators in this system. In both, the occupancy and detection plots, species are arranged in decreasing order of occupancy (also indicated by the size of the circle).

Fragmentation in the region

Based on the woodland cover and fragmentation analysis, we found that across our study area from 2007 to 2010, only 11.4 % of the 1 km² grids indicated loss of woodland cover, but from 2010 to 2015, 64 % of grids had lost more than 80 % of the woodland cover. With the loss of woodland patches, the landscape experienced considerable fragmentation, from 27 % of grids in 2010 having high fragmentation (LDI>0.75) to 49 % of grids in the year 2015. Between 2007 and 2010, there was a recovery in the woodland cover which may have been due to regrowth in the abandoned fallows (which also led to a decrease in fragmentation). But, from 2010 to 2015, the forest cover declined and more fragmentation occurred.

Model summary

Models for both taxonomic groups showed parameter convergence at the MCMC settings that we selected. The value of Gelman-Rubin convergence diagnostic for all posterior summaries (intercept and beta coefficients of species, community size and meta-community size) of both taxonomic groups was around 1, indicating sufficient

convergence and low Monte Carlo error (Gelman *et al.*, 1992). For mammals, the model containing LDI, the cubic term of LDI (LDI3), TWC and WC-loss as predictors in additive combination was selected as the best model, as it produced lower deviance compared to the model without the cubic term of LDI (ΔpD=1.5). For tree communities, the model without LDI3 had lower deviance (ΔpD=0.16) and hence was selected as the more plausible model.

Effect of fragmentation and woodland cover on species state

The effect of fragmentation and woodland cover varied between mammals and trees. Majority of tree species declined in abundance in response to fragmentation, and increased with quantity of woodland cover. The majority of mammal species did not show a significant response to fragmentation. Those that showed any significant response had a non-linear relationship with fragmentation, and no significant association with quantity and loss of woodland cover.

For trees, the average community-level abundance significantly reduced with LDI. At the species level, increased LDI was associated with a reduction in the abundance of 21 species and an increase in four (Figure 6). The declining species included key miombo species such as *B. boehmii* and *B. bussei,* and livelihood-important species such as *Terminalia sericea and Albizia adianthifolia*. Increasing species included *Piliostigma thonningi*, a rapidly re-growing species known to colonize clearings and fallow.

Increased TWC was associated with an increase in the abundance of seven species and a decline in two. The increasing species consisted of more woodland associated species such as *A. adianthifolia, Diospyros kirkii, Diplorhynchus condylocarpon* and *Te. sericea*.

In response to increased WC-loss, ten species declined and eight increased. The declining species included hard-wood species such as *Acacia nigrescens*, food-medicine species such as *C. collinum* and *Tamarindus indica*, and firewood species

such as *A. adianthifolia*. Increasing species consisted of food-plant species such as *Ficus stuhlmannii* and *Strychnos spinosa,* timber species like *Dalbergia melanoxylon and Te. Sericea*, and a miombo species, *B. boehmii.*

Thus, with 21 species declining with increasing LDI and only four species showing an increase, the effect of fragmentation on tree communities was largely negative. The amount of woodland cover (TWC) had a positive effect, with increasing TWC associated with increases in seven species and decreases in only two, whilst rises in the amount of woodland cover loss (WC-loss) generated almost identical numbers of species 'winners' and 'losers'.

For mammals, the community-level average occupancy (Ψ_μ) significantly increased with LDI (Ψ beta coefficient ± SD, 0.76 ± 0.37), and decreased with LDI3 (-0.33 ± 0.2) and TWC (-0.8 ± 0.35). Nine species showed significant responses to these two landcover variables (Figure 7). The probability of occupancy increased with LDI for 7 species, and that of two species declined with LDI3. TWC and WC-loss did not have any significant effect on occupancy of any of the mammal species, although both were associated with decline in all species.

The species which significantly increased with LDI consisted of domestic species (domestic dog, *Canis familiaris* and cat, *Felis catus)*, elephant shrews, murids (African spiny mouse, *Acomys sp.*, and thicket rat, *Grammomys* sp.) and species which are known to survive well in human influenced, disturbed and fragmented landscapes (lesser bushbaby, *Galago moholi*, and rusty-spotted genet, *Genetta maculata*). In addition, the African giant rat (*Cricetomys gambianus*) and South African hedgehog (*Atelerix frontalis*) reduced with LDI3.

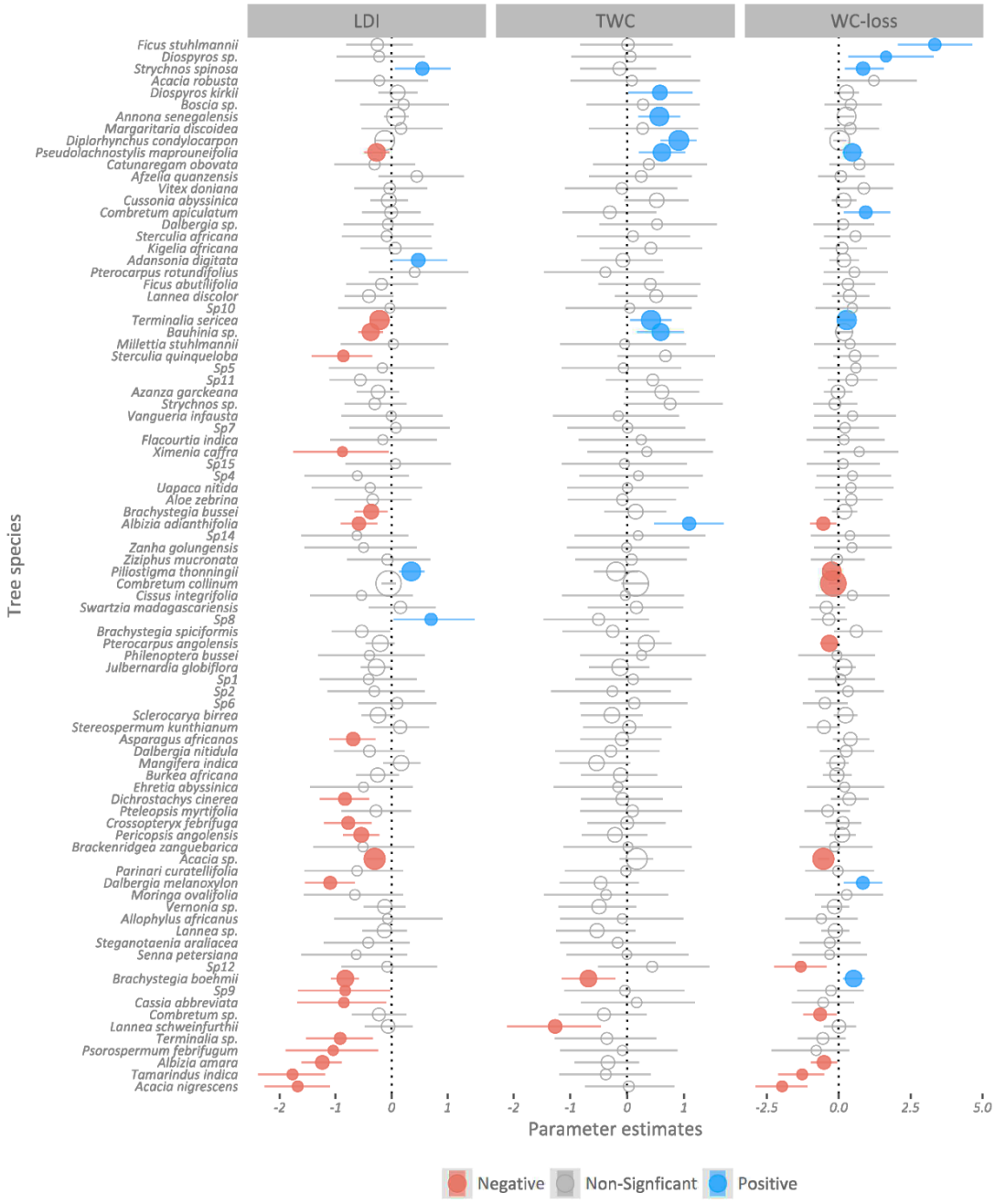


Figure 6: The coefficient plot of tree species' responses to the landscape division index (LDI), the residual of woodland cover and LDI (WC-res) and the residual of proportion of woodland cover loss and LDI (WC-loss), shows a largely negative effect of LDI and WC-loss on species abundance. The positions of the circles represent beta coefficients, the size of the circles indicates intercept (the mean abundance of species across the study area), horizontal lines on the circles show 95% CI, and colours signify the direction of the effect.

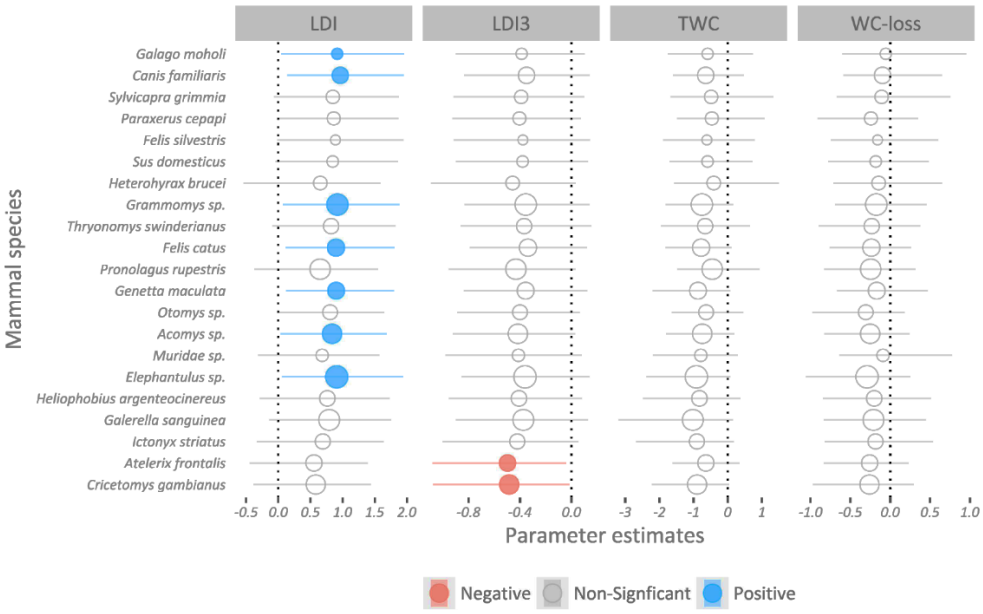


Figure 7: Models of mammal species occupancy to examine their response to landscape division index (LDI), the cubic term of LDI (LDI3), the residual of woodland cover and LDI (TWC), and residual of loss of woodland cover (WC-loss), suggest a possible nonlinear effect of LDI, since species increase (in blue circles) with the linear term of LDI and decrease (orange circles) with LDI3. LDI leads to increase in occupancy of elephant shrews, murids, domestic species and other species which are known to survive in human disturbed landscapes. The positions of the circles represent beta coefficients, the size of the circles indicate the probability of occupancy of the species across the study area, the horizontal lines on the circles show 95% CI, and colours signify the direction of the effect.

Effect of fragmentation and woodland cover on community state

At the community level, the species richness of mammals significantly increased with the linear term of LDI (30.5 ± 6 %) and declined with LDI3 (- 15.5 ± 7 %), the cubic term of LDI (Figure 8). TWC was associated with decreasing species richness (- 25 ± 10 %) and increasing beta diversity (19.5 ± 8 %) i.e. turnover in species composition of mammals. WC-loss did not have a significant effect on any of the community state variables of mammals. Among tree communities, LDI was associated with significant decline in species richness (-13.6 ± 6 %), increase in turnover (5 ± 2 %) and decrease in the nestedness component (-12 ± 3.5 %) of beta diversity. WC-loss and TWC had non-significant effects.

The species richness of mammals had weak and statistically non-significant (Moran's I= 0.05, p=0.07) while that of trees had relatively strong and significant

(Moran's I= 0.5, p<0.01) positive spatial auto-correlation. The predictor variables LDI (Moran's I= 0.54, p<0.01) and TWC (Moran's I= 0.48, p<0.01) also were spatially auto-correlated.

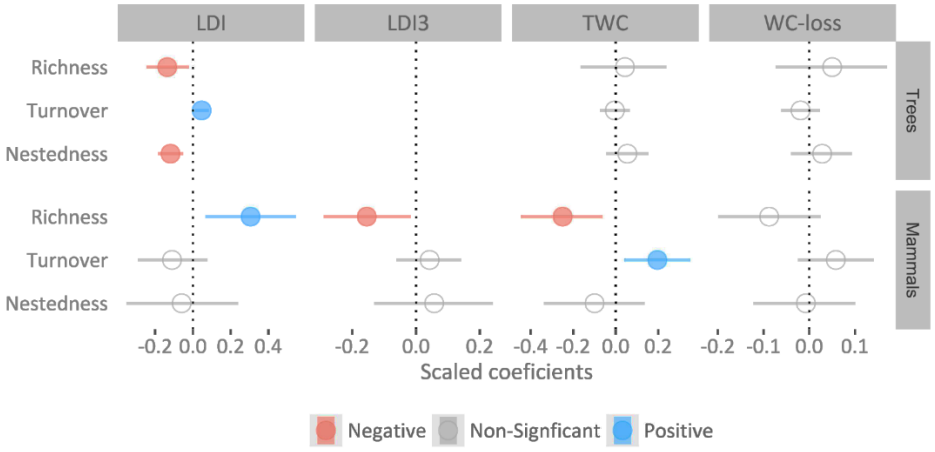


Figure 8: The coefficient plot of community state models, with circle positions representing scaled coefficients (proportion of deviation from the intercept), horizontal lines on the circles indicating 95% CI, and colours showing the direction of the effect. Increasing LDI reduced species richness of trees and affected mammal species richness non-linearly, showing a positive effect at intermediate levels and negative effects at the higher levels (LDI3). In addition, the residual of WC-LDI (WC-res) was associated with an increase in beta diversity of mammals.

Thresholds of fragmentation

In their global synthesis, Hooper et al. (2012) defined two levels of species loss: Intermediate (21-40% species loss) and High (41-60% species loss). Comparing the percentage of species losses observed during this study to the above levels, using the maximum species richness observed as a baseline, we state that tree communities declining continuously in species richness reach the intermediate level of species loss at about 25 to 50 % of fragmentation (LDI) and eventually reach the high level of species loss at about 85% of fragmentation (Figure 9). Mammals, on the other hand, are in the intermediate level of species loss at the beginning of fragmentation (8-25%) possibly due to hunting or other cofounding factors not observed in this study. They increase gradually in richness until the fragmentation is between 55 and 65%, and decline thereafter, reaching the intermediate level at 80% and the high level at about 85% fragmentation. We can thereby conclude that,

beyond 75% fragmentation, both taxonomic groups endure a high level biodiversity loss. As fragmentation and woodland cover in our study are highly correlated (R^2=0.77), the 75% fragmentation threshold translates to about 26.3 % (SE ± 1.3) of habitat quantity.

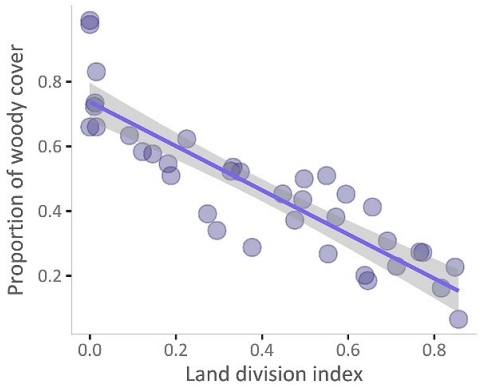
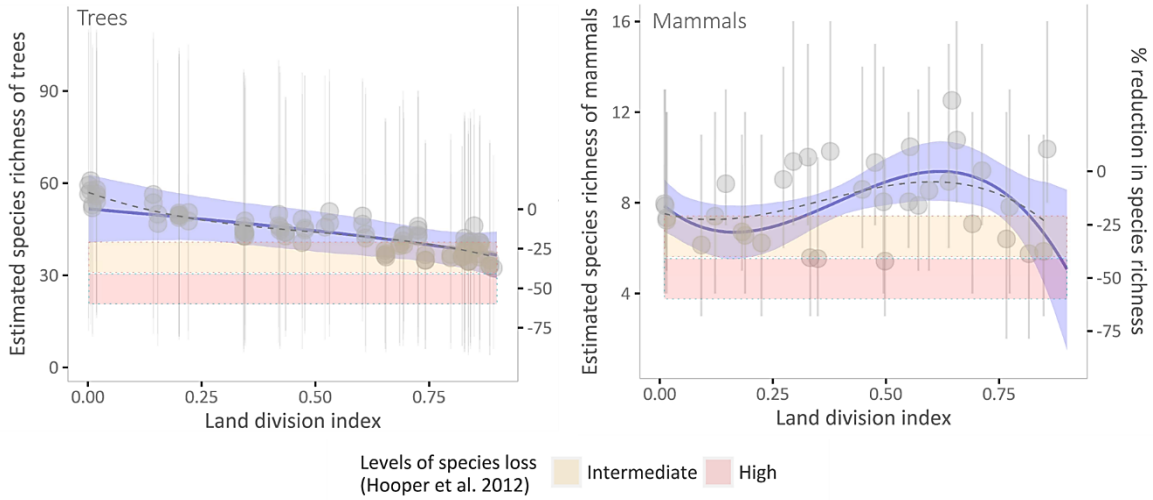


Figure 9: Land division index (LDI) with a significant negative relationship (R2=0.77) with the proportion of woody cover (TWC). The 0.75 threshold of LDI corresponded to 0.26.3 of woody cover.



10 *Figure 10: Relationship between fragmentation (LDI) and estimated species richness of trees (left) and mammals (right) in 1km² landscape units. Position of the circles denote point estimates with 95% CRIs (vertical lines) from the meta-community occupancy model. The grey dashed line is a spline smooth on the basis of point estimates. The blue line is a cubic regression line estimated by taking into account both the estimation error (posterior standard deviations) and residual variation around the regression line. The shaded area represents the 95% CRI of the predicted species richness. The yellow and red shaded areas show the levels of species loss described by Hooper et al. (2012), and the secondary Y axis shows % change in species richness from the maximum predicted species richness.*

Discussion

The socio-ecological miombo ecosystem is changing from an agriculture-woodland mosaic to a more simplified, production-oriented agricultural landscape. In the present study we demonstrated that fragmentation and reduction in woodland cover – possibly due to expansion of agriculture in our study area – result in reduction in diversity of the two taxonomic groups we studied. We further highlighted that the effect of fragmentation can be non-linear and vary between species and taxonomic groups. We found that while trees reduced in community size due to fragmentation, the mammal communities showed a non-linear response, increasing in richness up to an intermediate level of fragmentation and decreasing at higher levels. Mammal communities also underwent biotic homogenisation in response to woodland cover loss. We also identified the species 'losers' and 'winners', which can help to appraise the consequences of expansion in agriculture on ecosystem services, and to inform future conservation policies in this area.

We place the arrow of causality towards agricultural land use here, based on the assumption that the observed spatial patterns of landcover process (fragmentation and habitat loss), and the associated variation in ecological communities, are mainly determined by the expansion of agriculture. I can be confident in this assumption, given the wealth of data linking agricultural expansion with fragmentation and habitat loss (Wade *et al.*, 2003; Bogaert *et al.*, 2011), although, as far as we are aware, there have been no empirical studies to date on the causes of fragmentation in miombo woodlands. In addition, we are confident that our sampling was representative of the agriculture-induced fragmentation affecting miombo communities because: (i) we sampled landscape units representing a continuous gradients of fragmentation, amount of woodland cover lost (between 2007-2014) and quantity of woodland cover present (2014) in the landscape; (ii) our study area was a miombo landcover and an agricultural land-use-dominated landscape, and (iii) the sampling units were all within 50 km of one another, indicating that spatial variation by chance would be low.

Therefore, the study here demonstrates that agricultural expansion – via fragmentation and reduction in the miombo woodland cover – results in the following:

(a) At the species level: Declines in population size of most species, resulting in more species 'losers' than 'winners'.
(b) At the community level: (i) biodiversity loss by reduction in species richness, and (ii) changes in community composition.
(c) Group-specific responses caused by the inducing of different filtration processes.

We discuss these interrelated findings below.

Most species reduce in population size, with some showing a non-linear response to fragmentation

In the miombo region, the woodland patches have historically been cleared to create small (1-1.2 ha) farms, leading to landscape-level division of the woodland habitats. With increases in demand for agricultural land to expand the subsistence as well as commercial agriculture, the remnant miombo woodlands are experiencing further reductions in their continuity and quantity.

Our results underlined the disruptive effects of fragmentation on species populations, and further demonstrated the existence of linear and non-linear patterns of species response. We showed that the population size (abundance for trees, and occupancy of mammal communities) of the majority of species declined with increasing fragmentation, indicative of the '*more species losers than winners*' phenomenon (McKinney *et al.*, 1999). Our study further revealed that most mammal species showed a non-linear response, increasing in occupancy as fragmentation went from low to intermediate levels, but decreasing at higher levels of fragmentation.

The tree species that showed declines were primarily the miombo species (*Brachystegia boehmii and Brachystegia bussei*) and those used by humans for timber and firewood (*Dalbergia melanoxylon, Acacia nigrescens, Terminalia sericea, Pericopsis angolensis, Sterculia quinqueloba and Albizia adianthifolia).* While the decline of miombo species may be related to the loss of habitats, in addition along to harvesting by people, the decline of livelihood-relevant species may be more related to edge-effects that facilitate over-harvesting.

The miombo woodlands are considered to be low alpha diversity and population density ecosystems in context to fauna (Frost, 1996; Linzey *et al.*, 1997). Our results showed that the less fragmented and more heavily wooded landscapes had lower occupancy of most mammal species. Intermediate fragmentation and reduction in woodland cover positively affected the probability of occupancy of majority of mammal species. The increasing species consisted of the rapidly breeding *Elephantulus sp.*, and murids, generalist predators and domestic species. Assuming that the less divided, high-woodland-quantity landscapes are relatively undisturbed, our findings of a non-linear population response to fragmentation are similar to the results of Caro (2001) in miombo woodlands of western Tanzania, and studies in other ecosystems (Jeffrey, 1977; Andrén, 1994; Conde y Vera *et al.*, 2006; Cusack, 2011; Rich *et al.*, 2016). However, by showing that at higher levels of fragmentation most mammal species declined (significantly in the case of *Cricetomys gambianus* and *Atelerix frontalis*) and that the community-level average occupancy reduced, the results here expand upon and also validate the existence of non-linear relationships and possible thresholds as also observed elsewhere (Andrén, 1994; Hill *et al.*, 1999; Mönkkönen *et al.*, 1999; Pardini *et al.*, 2010) .

Additionally, the effect of fragmentation on individual species is known to be inconsistent and may be confounded by local contexts, such as hunting pressures and history of the landscape (Ewers *et al.*, 2006). The remaining woodland patches in the undivided landscape that we studied may have gone through defaunation due to hunting for bushmeat, as intact habitats are preferred by local hunters

(Timberlake *et al.*, 2009; Zach *et al.*, 2016), which may explain the lower densities of mammals in these areas. The observed non-linearity in response of mammal species would, in that case, simply be the result of multiple filtration processes: hunting causing shrinkage across all species (Reyna-Hurtado *et al.*, 2007; Hegerl *et al.*, 2015), and fragmentation leading to selection of smaller mammals, generalists and domesticated species (Jamoneau *et al.*, 2012; Keinath *et al.*, 2016; Zach *et al.*, 2016).

Community state: decline of species and changes in species composition.

Community-level effects on biodiversity are determined by the combination of species responses (Ewers *et al.*, 2006). As most individual species here showed a negative response to fragmentation, the community size (i.e. species richness) of both trees and mammals reduced with increasing fragmentation. The beta-diversity (i.e. species composition) response, by contrast, differed between the two taxonomic groups. The composition of tree communities changed in fragmented landscapes as the ubiquitous miombo woodland declined as the fast-growing secondary species, *Piliostigma thonningi*, became abundant. This combined effect of turnover and species loss because of the few 'winners', which were not abundant before replacing the many 'losers', which were the widespread species, results in 'subtractive heterogenization' (McGill *et al.*, 2015; Socolar *et al.*, 2016), and is represented in our result by increases in the turnover and loss of nestedness component of beta diversity of tree communities. The beta diversity of mammal communities did not show any significant response to fragmentation, but the quantity of woodland cover was associated with increases in the turnover component. At the species level, we did not find a statistically significant effect of woodland cover. However, at the community level, with a significant decrease in species richness and an increase in the turnover, the mammal communities in landscapes with higher quantities of woodland were associated with subtractive heterogenization – communities with fewer species and different compositions. However, as already discussed, the reduction in the size of mammal communities may be driven by bushmeat hunting

carried out preferentially in more continuous miombo patches. Furthermore, fragmentation at high intensities (less than 59.3 % connectivity-Andrén 1994) is more likely to be associated with the loss of habitat quantity (Andrén, 1994; Gutzwiller, 2002; Fahrig, 2003a, 2003b; Bennet *et al.*, 2010; Hanski, 2015), so we can further propose that higher levels of fragmentation involving loss of woodland cover may result in the loss of species along with reduction in beta diversity, causing subtractive homogenisation of mammal communities.

Difference between taxonomic groups: Mammals show a non-linear response while trees have a linear negative relationship with fragmentation

Results here demonstrated that the effects of fragmentation and habitat loss in miombo woodlands differ between trees and mammals. Although both taxonomic groups decreased in species richness, their responses varied depending on the level of fragmentation. Trees showed a linear reduction in number and drift in composition of species, whilst mammals increased in richness at lower levels of fragmentation and decreased at the higher levels. The non-linear response of mammals may be due to their ability to move and exploit resources in multiple fragments when the fragmentation is low and habitat patches are within reach (Pardini *et al.*, 2005). But as landscapes become more fragmented, both the size of remaining habitat patches and the overall habitat cover in the landscape reduce, leading to losses of resources and increases in competition and predation (Magrach *et al.*, 2014). However, it may also be possible that the non-linear response is due to reduced density and diversity of mammals in intact woodland patches due to over-hunting and resulting defaunation (Benítez-López *et al.*, 2017). Further, our study demonstrates that while tree communities undergo subtractive heterogenization as result of fragmentation, mammal communities experience subtractive homogenization in response to combination of fragmentation and woodland cover loss.

Fragmentation and woodland cover thresholds

For the two taxonomic groups combined, we identified a fragmentation threshold of 75%, which translated to the woodland cover (habitat quantity) threshold of about 26.3 % (SE ± 1.3), as fragmentation and woodland cover in our study are highly correlated (R^2=0.77). We therefore assert that beyond 75 % fragmentation or below 26% woodland cover, both taxonomic groups suffer a high level biodiversity loss. The habitat quantity thresholds of 26% in our study corroborates the similar habitat quantity thresholds (20-30%) suggested by Andrén (1994), Estavillo et al. (2013), Hanski (2015) and Fahrig (2003), among others. However, our result differs from the widespread notion that above the habitat quantity threshold (i.e. when the habitat quantity is more than 30%), the effect of fragmentation is non-existent. Here we emphasize that the taxonomic groups vary in their responses; with respect to mammals, we agree that fragmentation effects become less pronounced when habitat quantity remains above 30%, whereas for trees we disagree, and show that tree communities experience a linear decrease in population size and species richness, which is most likely due to loss of habitat and edge-related mortality.

All of the tree or mammal species that showed significant response to fragmentation or woodland cover were of least concern category as per the International Union for Conservation of Nature (IUCN, 2010). Although they may not be of international conservation significance, they do have local importance as they provide ecosystems services on which the livelihood of people depend upon(Ryan et al., 2016). The conservation of these species and maintenance of local biodiversity is thus important.

This study highlights the importance of the agro-ecological habitat matrix created by low-intensity agriculture in the miombo landscape in maintaining biodiversity. It shows that disturbance in this matrix due to expansion of agriculture results in decline in probability of species occupancy and alterations in the community structure and size at local scales. Thus, for biodiversity conservation this matrix, and

the land use activities that determine the spatial structure of the matrix, should be sustainability managed. The habitat quantity and fragmentation levels should be maintained in accordance to the thresholds suggested in this study. In addition, generalization and validation of these thresholds by undertaking multi-season and multi-spatial scale studies should be focus of future research.

Limitations of this study and future research

In this study, we could not fully distinguish between the effects of fragmentation and those of habitat loss, because the two variables were highly correlated. However, the use of residuals from models that included both will have allowed at least some separation of their effects. Testing the effect of woodland cover and fragmentation exclusively is important to understand the effect of the landcover processes on ecological communities. We used the areas with low fragmentation and high woodland cover as the baseline which led us to conclude that mammal communities respond non-linearly. However, the response of mammals may be confounded by the effect of hunting and other sources of disturbance. For a clearer understanding of the effect of fragmentation and habitat loss, the biodiversity of undisturbed, less divided and large miombo woodland patches in similar climatic and topographic conditions should be the reference point for community size and integrity. We excluded the high-elevation landscapes which had relatively undisturbed woodland areas, as they were inaccessible and not-preferred for farming. But these woodland patches, although mainly non-miombo, may be the last remaining undisturbed refuges supporting fauna that have migrated from the disturbed and fragmented landscapes. Accounting for the role of these high elevation habitats will be important to understand biodiversity change in this region. Lastly, this was a single-season study, and there is a possibility that there may be between-season variation in mammal activity, density and diversity which may have influenced our estimates.

Thus study employed camera trapping, a widely used technique to study mammal communities (Rovero et al., 2013). There can be a concern that choice of the survey design - placement strategy of camera traps - may influence the estimates and thereby the inferences made in this study. The placement strategy can be broadly classified in to: (i) non-random placements along the target locations – trails, roads, water points and salt licks, and (ii) random placements determined a priori by geographical coordinates (Cusack et al., 2015). In this study the approximate location of the camera traps – the centre of the grid – was selected randomly. However, the exact camera placement was determined by specific features such as open and frequently used pathway to increase capture probability. Thus, we employed semi-random placement of cameras. In the random design, such features are sampled in proportion to their occurrence in the landscape and therefore they may avoid bias associated with sampling along the preferred habitat features (Harmsen et al., 2010; Cusack et al., 2015). Studies (Bitetti et al., 2014; Blake et al., 2014) claim that random and non-random camera location may result in contrasting conclusions. However, these studies are from forested habitats, and they compared camera placement strategies in different locations and confounding with the effects of habitat heterogeneity (Cusack et al., 2015). Cusack et al. (2015) carried out a paired comparison of the random and non-random camera placements in dry open tropical ecosystem in Tanzania and showed that with adequate sampling (>1400 camera trap days) placement strategy does not affect community level inferences. Further, they demonstrated that trail based sampling improves detection of more elusive species. This study consisted of 1665 camera trap days on average (45 mean number of days X 37 camera traps) and thus the likelihood of it being biased in the community level inferences is low. In addition, the trail based sampling designed for community level occupancy studies like ours may reduce the habitat-feature bias to some extent by decomposing heterogeneity in detection frequencies to binary presence-absence (Mackenzie et al., 2005).

In this study we used space-for-time substitution and selected a chronosequence of LSUs representing a spatial gradient of fragmentation and woodland cover quantity. Such a sampling design is disposed to spatial autocorrelation (Diniz-Filho et al., 2003; Warren et al., 2014). This study had a positive spatial auto-correlation for tree communities meaning the nearer LSUs had similar levels of species richness. The predictor variables (fragmentation and quantity of woody cover) were also spatially structured. Therefore, the effect of fragmentation and woody cover loss on tree communities is spatially confounded. The difference in spatial auto-correlation between trees and mammals could be because of the difference in ways in which the LSUs were selected. The tree LSU were randomly selected and contained higher proportions more disturbed sites. Their distribution was biased towards higher values of fragmentation and lower values of woodland cover quantity and species richness. In case of mammal LSUs, which were selected to represent all classes of fragmentation, the distribution was uniform and was influenced by the highly affected sites. When the site selection is influenced by the more disturbed sites, the relationship between disturbance and diversity are more likely be spatially confounded as the land use driven disturbance, the predictor, itself is spatially structured (Diniz-Filho et al., 2003; Ahrends et al., 2010). The results here demonstrate the spatial mechanisms that structure both, agriculture expansion led fragmentation and loss of woodland cover, and diversity of tree communities.

Conclusions

Our study demonstrates that the fragmentation and the associated loss of woodland cover – possibly due to agricultural expansion in the socio-ecological miombo landscape – results in reduction in population size of species. Further, we conclude that at the community level, species losses result in reductions in community size and changes in community composition. We also show that different taxonomic groups respond differently to the landscape processes. Trees undergo subtractive heterogenization with reduction in community size and drifts in composition, while mammal communities experience subtractive homogenisation due to reduction in

community size, combined with decay of species dissimilarity. Finally, we identity 75-85 % as a fragmentation threshold (or 20.6 to 26.3 % of habitat threshold) beyond which communities experience intermediate (21-41%) to high-level (41-60%) species loss, which may have disruptive effects on ecosystem functioning and provisioning of ecosystem services. To manage biodiversity within the agricultural landscape and to mitigate biodiversity loss, we therefore recommend that, at the scale of 1km^2, at least 30% of woodland cover, with no more than 75% fragmentation, should be maintained.

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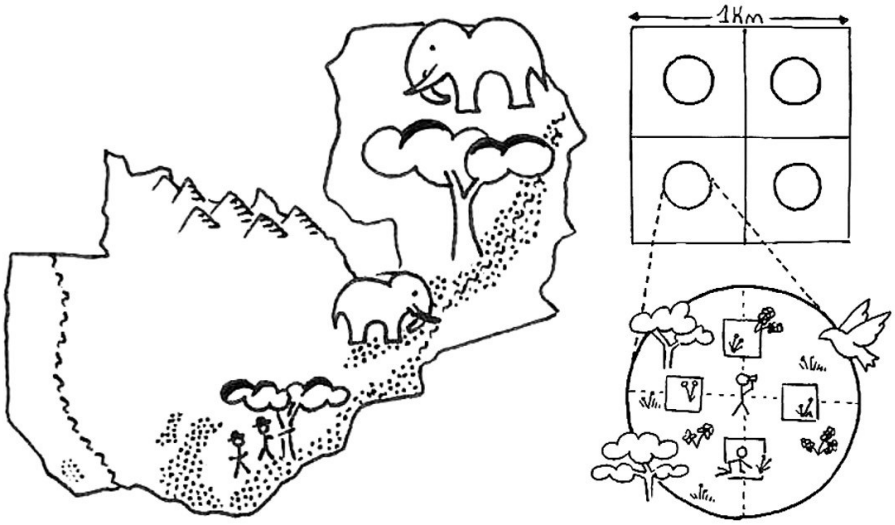
Chapter 4

Effect of human and elephant disturbance on habitat structure and diversity of birds in the mopane woodlands.

Hemant G. Tripathi, Casey M. Ryan, Tiwonge M. Gawa



This chapter is intended for split publication post submission. It will be divided in to two sections: (a) Effect of disturbance on habitat and (b) Effect of disturbance on diversity.

HGT conceived the research questions with inputs from CMR. HGT, CMR and TMG (Percy FitzPatrick Institute of African ornithology) developed the study design. HGT collected the vegetation data and TMG collected the bird data. HGT collated and analysed the data, and wrote the manuscript. CMR provided suggestions for analysis and comments on the manuscript.

Abstract

Aim: Humans and elephants influence the structure of savanna woodlands of southern Africa. Due to increasing land use pressures and consequent habitat loss, in addition to hunting, the historical elephant ranges have shrunk and their populations are now restricted to the few protected areas or regions of low human dominance. Removal of woody biomass by humans in the human-dominated areas and elephants in the protected areas modify habitat structure and alter biodiversity of the woodlands. However, their effect can be different. Comparison of the effects of elephants and humans will improve our understanding of how land use mediated changes are shaping the savanna woodlands.

Location: Mopane woodland cover in Zambia.

Methods: In this single-season spatial comparison, we identified the structural forms of the mopane woodland in Zambia using hierarchical clustering. We examined relationships between habitat attributes, species and functional diversity of bird communities, and intensity of human and elephant disturbances using mixed models. We used deviation from the intercept to compare the effect sizes of significant predictors.

Results: We identified three distinct structural forms of the mopane woodlands and found that elephant and human disturbances were associated with different forms. The effect of elephant disturbance on stand density (-7.1%) was greater than that of humans (-4.1%). In spite of the greater reduction in stand density, elephant disturbance did not reduce the total basal area (woody biomass), whereas human disturbance significantly reduced it (-13%). The negative effects of both disturbances on species richness of birds were identical (Human= - 4.3%, Elephant= - 5.5%). Bird communities became more similar in species (6.7%) and functional compositions

(7%) with elephant disturbance. Functional diversity of birds reduced with human disturbance (- 4.2%) but did not significantly change with elephant disturbance.

Main conclusions Humans and elephants lead to different structural forms and affect habitat attributes and bird-diversity in dissimilar ways. Humans reduce woody biomass, while elephants do not. Human disturbances result in loss of species and functional diversity in bird communities, while elephant disturbance leads to subtractive biotic homogenization with no loss of functional diversity.

Keywords Africa, mopane woodland, savanna, tree removal, elephant, human, birds, diversity, functional diversity, alpha-diversity, beta-diversity, Zambia

Introduction

Land use change is known to alter biodiversity by reducing the quantity (Foley, 2005; Estavillo *et al.*, 2013) and modifying the structure of habitats (Pardini *et al.*, 2005; Seymour *et al.*, 2010; Sitters *et al.*, 2014). Removal of woody biomass by humans is a dominant land use activity (Chidumayo, 1993; Ryan *et al.*, 2014; Woollen *et al.*, 2016), and, along with elephant herbivory (Cumming *et al.*, 1997; Guldemond *et al.*, 2008), is a major determinant of habitat disturbance in the savanna woodlands of southern Africa (Mograbi *et al.*, 2017). Humans and elephants appear to have similar effects on habitat structure. However, there are inherent nuanced differences in ways in which they target and remove trees (Mograbi *et al.*, 2017). Due to these differences, they may affect the habitat attributes of the woodland and its biodiversity in dissimilar ways. Comparison of effects of these two dominant habitat determinants has, surprisingly, received little attention. In the study here, we present a spatial comparison of the effects of tree removal by humans and elephants on (i) structural attributes of the woodland habitat and (ii) diversity and composition of species and functional traits of bird communities in the mopane woodlands of Zambia.

Savanna woodlands are the dominant vegetation cover in the southern hemisphere. They are dynamic ecosystems characterized by the dominance of trees with a sparse understory of grasses (Scholes *et al.*, 1997) maintained by the combination of factors – herbivory, anthropogenic fires and unimodal low rainfall (~1000 mm; Pringle et al. 2015, Sankaran et al. 2005, Bond & Keeley 2005). These woodlands are now also subjected to modifications due to the increasing intensity of land use and land cover change (Aleman *et al.*, 2016). The land use mediated changes in structure and distribution of these woodlands can affect their important biodiversity consisting of distinct species with a high degree of endemism (Mittermeier *et al.*, 2003; Murphy *et al.*, 2016; Newbold *et al.*, 2017). In addition, these woodlands are underrepresented in the global biodiversity datasets and the global biodiversity-land use discourse (Newbold *et al.*, 2017; Vellend *et al.*, 2017). To effectively understand how land use is organizing global biodiversity at local scales, it is therefore important to investigate the African savanna context of how land use mediated changes are modifying habitats and altering their biodiversity.

Disturbance and habitat modification

Humans and elephants have been an integral and ancient part of the African savanna biome (Ellis, 2011; Charles-Dominique *et al.*, 2016). Humans through low-intensity land use and fire (Ellis, 2011), and elephants through herbivory (Laws, 1970) have influenced woody cover in the savanna woodlands in the past. However, in recent times, the relative influence of the historical disturbances have changed. In southern Africa, increasing rural and urban human densities and their demand for woodland products – fuelwood and charcoal have intensified wood harvesting (Hosier, 1993; Higgins *et al.*, 1999; Kalema *et al.*, 2012; Ryan *et al.*, 2016; Sedano *et al.*, 2016). Further, habitat loss due to expansion of croplands (Ryan *et al.*, 2012, 2014; Rudel, 2013) and hunting, mainly for trade (Cumming et al., 1997), has pushed elephant populations towards less human-disturbed regions – small network of protected areas and game reserves, confining and concentrating their impact (Hoare *et al.*, 1999; Boer *et al.*, 2013; Chase *et al.*, 2016). Humans have also reduced the

intensity of fires and altered fire frequencies for effective land use management (Archibald *et al.*, 2012). The frequency and spatial extent of high-intensity fires, the key determinants of savanna structure associated with high mortality of trees, have been reduced to avoid damage to crops, while frequent low-intensity fires to smaller spatial extents have been specifically used by humans to harvest trees and create pastures(Archibald *et al.*, 2012; Kamau *et al.*, 2014; Archibald, 2016; Andela *et al.*, 2017). Hence, with reductions in the intensity and thereby the influence of fire, humans and elephants now have stronger influence on the proportion of woody cover and the overall structure of savanna woodlands in Africa.

The mopane woodlands, composed of the mono-specific stands *Colophospermum mopane* (Kirk ex Benth.) Kirk ex J. Léon, are the second most dominant woodland habitat after miombo woodlands in subtropical southern Africa (Timberlake *et al.*, 2010; Shorrocks, 2015). They cover about 0.4 million km^2 (30-35 % of savanna in southern Africa) and are adapted to stresses related to drought, fire, and browsing by animals (Frost *et al.*, 1996; Timberlake *et al.*, 2010; Mapaure *et al.*, 2011). The mopane woodlands commonly occur in low-lying regions (500 to 800 m) and in a wide range of soils (Sebego, 1976; O'Connor, 1998; R. A. Makhado *et al.*, 2014; Stevens *et al.*, 2014). In the nutrient-rich and alluvial soils, the woodlands are mostly composed of trees of 6 m to 25 m tall with broad canopies, the *cathedral mopane*, while in shallow sodium-rich clay soils with high water holding capacity they exhibit a stunted form, the *shrub mopane* with most trees up to 1.5 m (Sebego, 1976; Davis *et al.*, 2014; R. A. Makhado *et al.*, 2014). Within the limits set by the edaphic and climatic factors, the two major disturbance factors: (i) browsing by mega-herbivores, mainly elephants, and (ii) selective harvesting by humans, determine the variation in the structure and the diversity of the mopane woodlands (Hempson *et al.*, 2007). These disturbance factors can be broadly linked to two land use types: (i) protected areas, mainly national parks, where browsing by mega-herbivores is a dominating feature, and (ii) the human-dominated areas, where selective logging mainly for charcoal, firewood and timber is a major disturbance.

In the protected areas, mopane woodlands provide a consistent supply of nutritive feed throughout the year (Styles *et al.*, 1997; Lagendijk *et al.*, 2005; O'Connor *et al.*, 2014). The large herbivores such as elephants (Lagendijk *et al.*, 2005), kudu (Hooimeijer *et al.*, 2005) and eland (Styles *et al.*, 2000) browse upon the foliage, stems and twigs by pushing over, uprooting and snapping, and this leads to the creation of disturbed shortened mopane stems, the *mopane morphs* (Styles *et al.*, 2000) which in response to extensive browsing produce nutritious and more accessible leaves attracting small ungulates (Styles *et al.*, 1997, 2000) and also other biodiversity.

As most of the browsing activity may often be restricted to the morphs, the unaffected mopane stems in the surrounding areas may survive and become bigger in size (mean DBH > 35 cm, height >12 m; Kohi *et al.*, 2011). Depending on the intensity of use, the mopane landscape created by such browsers are maintained in a spatially heterogeneous state consisting of large stems alongside the *mopane morphs* (Kohi *et al.*, 2011). It is possible that, at high-densities, the large herbivores may over exploit the *mopane morphs* and subsequently migrate, leaving the particular woodland to recover (Styles *et al.*, 2000). Conditional upon other factors such as fire, rainfall and human disturbance that control the woodland structure, this may result in regeneration and, depending on the return of large herbivores, alternating stable states of the woodland (Smit, 2001; Gandiwa *et al.*, 2009).

In the human-dominated areas, the mopane woodland is used as a livelihood resource for human-communities living within or near the woodland as it provides medicine, food, timber and non-timber products (Mashabane et al. 2001; Makhado et al. 2014; Makhado et al. 2012; Makhado et al. 2009; Ryan et al. 2016). The most important land use, however, is of extracting fuelwood as the mopane wood produces good quality slow-burning charcoal and thereby is preferred and selectively harvested for local and commercial use (Chidumayo, 1993; Wessels, 1999; Chidumayo *et al.*, 2013; Woollen *et al.*, 2016). Selective logging for fuelwood results in a reduction of density of large stems and increase in density of small and undesired or coppicing stems (Mapaure *et al.*, 2011; Chidumayo *et al.*, 2013).

Both the selective logging by humans and browsing by elephants are known to reduce the density of stems (Mograbi *et al.*, 2017). However, they may have dissimilar effects on the other attributes of the woodland habitat such as stem-size, basal area, structural diversity and vegetation diversity. Studies by Staver & Bond (2014) and Asner & Levick (2012) show the existence of a size threshold (1-5 m height) beyond which the stems are less vulnerable to elephant damage. No such known threshold exists for human activities as large and small stems, and even the coppicing stems are known to be used in high-intensity land use (Malimbwi, 2005). Another fundamental difference between the elephant and human impact could be that elephant disturbance is driven by geological patterns and distribution of surface water, while human disturbance is determined by the ease of access (Mograbi *et al.*, 2017). Due to different ways of using the woodlands, humans and elephants may impose different types of top down stress and modify habitat structure in dissimilar ways. The modifications in the structural attributes of the habitat alter microhabitat conditions: canopy cover and light intensity, influencing the diversity and composition of the trees and understory (Beuchner *et al.*, 1961; Cumming *et al.*, 1997; O'Connor *et al.*, 2014; Coverdale *et al.*, 2016). To summarize, human and wildlife disturbance modify the structural and diversity attributes of the woodland habitat, possibly in different ways (Mashabane *et al.*, 2001; Gandiwa *et al.*, 2009; Ferguson, 2014).

Disturbance and biodiversity

The changes to the habitat attributes can have cascading effects and influence the animal communities (Cumming *et al.*, 1997). Habitat alteration results in bottom-up effects which alter diversity and composition of species and functional traits (Seymour *et al.*, 2010; Püttker *et al.*, 2015). Studies about how habitat modification by elephants and humans affect biodiversity in the African savannas are few (elephant=Cumming et al. 1997; Fenton et al. 1998; Herremans 1995; Botes et al. 2006; Bonnington 2012, human=Kalaba et al. 2013; Jew et al. 2015; Kalema & Witkowski 2012; Newbold et al. 2017). Most studies about the effect of human-led

habitat disturbance on biodiversity point towards negative effects (Newbold et al. 2017, and references therein). In comparison, understanding of how elephant disturbance affects biodiversity is contentious (Kuiper *et al.*, 2014). Cumming et al. (1997) highlighted this uncertainty by showing that although bird and ant richness was significantly lower in elephant-disturbed compared to intact woodlands, species richness of woody plants, bats or mantids was no different. Among other studies, O'Connor & Page (2014) demonstrated a decline in tree richness, while, Coverdale et al. (2016) underlined positive effect on understory richness.

Herremans (1995) found no change in richness but alteration in the composition of bird communities, whereas, Bonnington (2012) noted the greater diversity of butterflies in response to elephant disturbance. One of the noticeably common observations in the elephant disturbance - biodiversity studies with contrasting findings (Herremans, 1995; Cumming *et al.*, 1997) was the decline of habitat specialist species in the elephant impacted areas. This points out towards the multi-faceted nature of biodiversity change. The communities may show contrasting species and functional-trait patterns in response to disturbance (Flynn *et al.*, 2009; Forrest *et al.*, 2015). They may lose many species but yet retain the overall functional diversity because the lost species were functionally redundant (Flynn et al. 2009; e.g. Edwards et al. 2013). Communities may also undergo dramatic reduction in functional diversity even after losing only few species, which are disproportionately functionally unique (Flynn et al. 2009; e.g. Forrest et al. 2015). Therefore, studying biodiversity change from a functional diversity perspective can reveal more about community assembly processes and help understand how species respond to disturbance. In conclusion, understanding of how elephant disturbance affects species and functional diversity is obscure.

Given the above, we hypothesized that elephant and human disturbances affect different attributes of the mopane woodland habitat and may be associated with different structural forms of the woodland, and as consequence, they will have dissimilar effects on species and functional diversity. To examine this, we

investigated how the two disturbances affect the structural attributes and structural composition of the mopane woodlands and how such habitat modifications organize the species and functional diversity of birds at alpha and beta diversity levels.

We asked the following questions:

a) How does human and elephant disturbance affect habitat structure?
    i. What are the major structural forms of mopane woodlands? Are they related to human and elephant disturbance?
    ii. Which attributes of the mopane habitat are affected by the human and elephant disturbance?
b) How does human and elephant disturbance affect bird communities?
    i. How does disturbance due to humans and elephants affect species diversity?
    ii. How does disturbance due to humans and elephants affect functional diversity?
    iii. Which species and functional traits are affected by humans and elephants?

Methods

Approach

To answer the above questions, we performed a spatial comparison of indicators of disturbance, habitat structure and species and functional diversity of bird assemblages. We employed hierarchical clustering to identify the structural forms of the woodland. We used linear mixed models to examine the effects of disturbance on habitat attributes, and effects of disturbance and habitat attributes on species and functional diversity of birds.

Study area

We carried out this study during the dry season (May – July 2015) in the mopane woodlands of Zambia which mainly occur in the eastern part of the country from north to south covering Luangwa, Luano and Zambezi valleys (Figure 1). The study area consisted of three major national parks – North Luangwa, South Luangwa, and Lower Zambezi. In the national parks, the woodland is an important habitat for elephants. Outside the parks, people use it as a resource for fuelwood, building materials, food, and medicine.

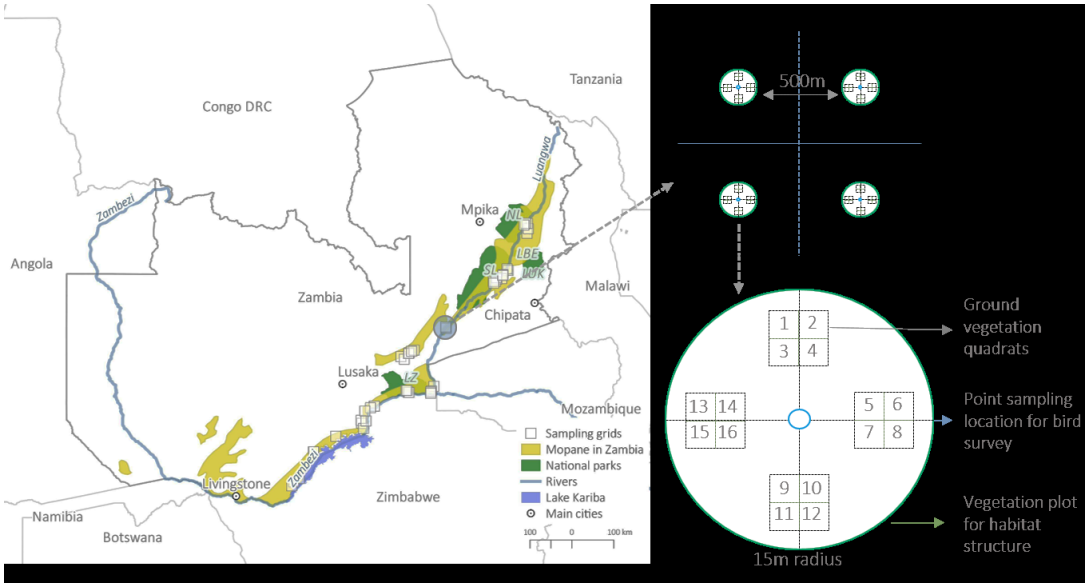


Figure 1: Distribution of sampling grids in the mopane woodlands of Zambia (left) with national parks (LZ= Lower Zambezi, SL=South Luangwa, NL=North Luangwa, LZK=Lukusuzi, LBE=Luambe), the basin of two major rivers (Luangwa and Zambezi), Lake Kariba and main cities around the sampling area. Each 1 km² grid consisted of four circular sampling plots 500 m apart (right). The plots were used for sampling of vegetation structure and to measure disturbance by counting number of stems affected by humans and elephants. At the center of plot, an incidence survey of bird species was undertaken. Within each plot, four 1 m² quadrats were used for a ground vegetation survey.

Data collection

We collected habitat structure and disturbance data using circular plots and bird diversity data using point counts. The sampling units were nested within squares (grids) of 1 km² size spread across the mopane woodland cover in Zambia.

Sampling units

Using White's African vegetation map (White, 1983), we identified the mopane woodland cover in Zambia. Before going to the study area, we randomly selected 100 grids of 1 km^2 across the mopane landscape such that the grids were at least 250 m away from any tar road, big rivers or waterbody, 1 km away from each other and have average altitude below 750 m. During the field study, from this pool of grids, we sampled 45 grids for habitat related parameters (habitat structure and diversity). Within 26 of these 45 grids, we sampled bird diversity. Each grid contained four circular plots of 15 m radius, 500 m apart. These circular plots were used for collecting habitat data. The center of the circular plots was used for bird surveys using point count. In total, we sampled 178 plots for habitat structure and 120 plots for avian diversity clustered in 45 (one of the grids had only two plots) and 30 grids respectively.

Habitat structure and diversity

In each circular plot, we identified genus and species, measured DBH (diameter at breast height, 1.3 m) and height of all stems above 10 cm DBH and counted the total number of stems below 10 cm DBH. To estimate ground cover and ground vegetation diversity, we used four smaller quadrats of 1 m^2 placed within the circular plot, one in each cardinal direction, and at a distance of 10 m from the center of the plot. Each ground cover quadrat was sub-divided into 4 blocks such that in each circular plot, the ground cover quadrats together represented a total of 16 blocks. Ground cover was then estimated as the total number of blocks occupied by ground vegetation in each plot. For each of the ground vegetation species, the total number of blocks they occupied was used as the index of abundance (abundance here on).

Using the field data, we computed the following six parameters to represent habitat structure:

1. Mean DBH: For mean DBH (cm) we used the quadratic mean diameter derived by averaging the squared DBH of all stems >10 cm. The quadratic mean is the measure of average tree size which is essentially the mean basal area of stem and is calculated by $D_g = \sqrt{\frac{\sum_{i=1}^{n} d_i^2}{n}}$
2. SD: Stand Density (stems ha^{-1}), the total number of tree stems >10 cm DBH.
3. SD-small: Density of small stems (stems ha^{-1}), the total number of tree stems <10 cm DBH.
4. BA: Basal area (m^2 ha^{-1}), calculated as a total area occupied by stems >10 cm DBH.
5. GC: Ground cover, relative proportion of the total number of blocks covered by ground vegetation.
6. SDH: Structural diversity, the sum of diversities of DBH (bin size = 10 cm) and Height classes (bin size = 2 m) in each plot using the Shannon diversity index (Shannon 1948; Magurran 2004).

For the diversity component of the habitat, we used alpha diversity (Shannon) and beta diversity (turnover) of trees and ground cover plants. Alpha and beta diversity of trees were positively correlated (R2=0.35), and alpha and beta diversity of ground cover species were negatively correlated (R2=0.72). To reduce the number of parameters, we subjected the four diversity variables to principal components analysis (PCA) and selected the first two axes which represented 86.7% of the total variation among them (PCA bi-plot provided in the supplementary material). The first axis accounted for 50.5% variability and was associated increase in alpha diversity and a decrease in beta diversity of ground cover species. The second axis explained 36.2% of the variation and was negatively associated with alpha and beta diversity of trees. For ease of interpretability, we inverted the second axis by multiplying it with -1. The two orthogonal PCA axes thus indicated the following parameters:

7. GC-div: PCA axis 1 indicating an increase in species diversity and a decrease in beta diversity of ground cover plants.
8. TR-div: PCA axis 2 indicating an increase in alpha and beta diversity of trees and alpha diversity of ground cover plants.

Disturbance and environment variables

As an indicator of disturbance, we used two groups of variables: the observed impacts and unobserved indirect impacts. The observed impact at each plot level was measured by counting the total number of stems which are stunted, debarked, cut or coppiced. The stunted, pollarded or debarked stems with a clear sign of animal impact were considered as an indicator of large-herbivore, primarily elephant, related impact. The cut stems were accounted for as a human impact. The number of impacted stems were transformed into relative percentages of the total number of stems found in the plot. Here onwards, the percentage of cut stems is denoted by *HI* and indicates human related disturbance, and percentage of stunting, pollarding or debarking is denoted by *WI* and indicates mainly of elephant related disturbance on mopane stems.

The indirect impact is derived from the distance-based attributes which can indicate a potential effect of humans or wildlife. Based on the literature, we have an a priori belief that the areas near or within protected areas and water bodies are more likely to be impacted by wildlife (Fullman, 2009) while locations away from the protected areas and closer to the roads and populated locations may mainly be affected by humans (Thiollay, 1999; Hosaka *et al.*, 2014). We used five variables to account for unobserved disturbance: distance from road, standing water, stream and populated area, and protected area status. As these variables were correlated, we performed a PCA to reduce the number of variables to an orthogonal set of three. Results from the PCA indicated that the first three axes explained 82% of the variation in the five variables (PCA bi-plot provided in the supplementary material). Based on the factor loadings, PCA axis 1 represented a gradient of increasing distance from the stream and decreasing distance from big standing water bodies, the absence of protected

areas and decreasing distance from populated areas. PCA axis 2 showed the decreasing distance from streams and standing water bodies, the presence of protected areas, increasing distance from populated areas and decreasing distance from the roads. PCA axis 3 indicated the increasing distance from streams and standing water, the absence of protected areas, decreasing distance from roads and increasing distance from populated areas. In all, the PCA axes 1, 2 and 3 mainly indicated the effects of populated areas, protected areas, and remote unprotected areas, we term these axes as Populated, Protected and Remote.

Sampling of bird communities

We chose birds as the taxonomic group for this study because they are comparatively the most understood class of organisms (Bibby, 1999), are sensitive to habitat modifications (Owens *et al.*, 2000) and are good indicators of effects of habitat filtering process as the chances of variation in bird diversity being confounded by hunting pressures is lower than mammals (Benítez-López *et al.*, 2017).

The bird data in this study were collected at each circular plot by the single visit point sampling presence-absence survey method. The center of the circular plot was used as the survey point and the bird species seen or heard during the sampling period of 15 minutes were listed. Bird surveys were done between 6 - 9 am (about 15 minutes after sunrise) for each grid to reduce variation due to the time of sampling as bird activity tends to vary with time of the day (Gregory *et al.*, 2004). Four species could not be identified during the study.

Functional trait data

Trait information for species observed in this study were derived from Elton Traits 1.0, a global species level database prepared by Wilman et al. (2014). The trait values were the relative importance (%) of different categories of diet, foraging strata and habitat (Table 1).

We further calculated species level index of specialization for each trait category (diet, foraging strata, and habitat) using the inverse of Shannon diversity index. The lowest values of Shannon diversity of traits indicate the highest specialization. Specialization index was multiplied by 100 for easier interpretation.

For the four unidentified species in our study mean values were used (We also conducted the whole analyses by removing the unidentified species but this did not make any significant difference so results from using the mean values are presented).

Table 1: To examine trait diversity and composition of bird species in response to variations in habitat structure, we collected life history and ecological trait (referred as trait hereafter) data of bird species encountered during this study. The traits included in this study are given below.

Trait category	Trait levels	Data type (unit)
Diet	Invertebrates, Vertebrates, Scavenger, Fruit, Nectar, Seed, Other plants, Water	Percentage of the total diet group
Foraging strata	Ground, Understory, Mid high, Canopy, Aerial	Percentage of the total foraging strata group
Habitat	Forest, Savanna, Shrubland, Grassland, Wetlands	Percentage preference for the habitat
Body mass		Continuous (kg)
Specialization group	Habitat, Diet, Foraging	(1/ Shannon index) *100

Diversity calculations

Using the species incidence data and the functional trait information of species from the databases, we computed alpha and beta level measures of species and functional diversity. For the beta diversity measures, we followed the multi-component partitioning framework of Baselga (2010) where beta diversity can be decomposed into the turnover and nestedness component. Turnover represents the true transformation of a community due to replacement of species or functional groups (Legendre *et al.*, 2013). Nestedness indicates sub-setting of communities due to loss

of alpha and beta diversity (Ricotta *et al.*, 2008; Ulrich *et al.*, 2012; Cardoso *et al.*, 2014).

Alpha and beta diversity of species

We estimated species richness as a total number of unique species observed as present in each plot. Species richness measure in this study is conditional upon the assumption that since sampling effort was constant the bias due to imperfect detection would be uniform.

Beta diversity is a measure of variability between communities in species composition and is calculated on the basis of pairwise dissimilarity in species presence between communities (MCD). We calculated MCD using the incidence based multi-component beta diversity (Baselga, 2010). The multi-component beta diversity is calculated using Sørensen dissimilarity and contains two components, the Simpson dissimilarity accounting for "turnover" (MCD-turn) and the difference between Sørensen and Simpson dissimilarity accounting for "nestedness" (MCD-nest).

Alpha and beta diversity of functional trait groups

We used the distance-based measure of functional diversity (FD) to compute the mean functional distance (MFD), a measure of mean trait dissimilarity between species and is explicitly based on the mean pairwise distance between species in a community. MFD here is similar to the other widely used distance-based Rao's quadratic entropy Q (Laliberte et al., 2010) and the dendogram-based FD index (Petchey & Gaston 2002) and, likewise, indicate the functional space that species collectively occupy in a community (Petchey et al., 2006; Swenson, 2014). Rao's quadratic entropy (Rao), the widely used distance-based index, is an abundance weighted measure of functional diversity. MFD, the index used in this study, can be a considered as a incidence version Rao (Pavoine et al., 2011). We used MFD as it is more flexible, like the multi-dimensional functional indices of Villéger et al., (2008), it does not require more species than traits (Laliberte et al., 2010) and is easy to

interpret as it is expressed in terms of distance ranging from 0 to 1 indicating lowest and highest possible values of functional diversity.

To compute MFD, we subjected the standardized trait matrix (14 traits) to PCA and selected the first 10 axes which explained ~95% of the variation in trait composition (PCA biplot attached as supplementary material). All of the functional trait variables here were continuous, and so we used Euclidean distance on standardized and scale transformed variables.

Functional beta diversity, the pairwise dissimilarity in functional space is conceptually based on the tree based phylogenetic and functional beta diversity measurement described by Melo et al. (2014) which was adapted to suit Baselga's (2010) beta diversity framework by Leprieur et al. (2012). To compute the functional beta diversity, we used the selected PCA axes of traits and created a functional dendrogram using the Ward clustering method. In the dendrogram, species are represented by the nodes and the length of the dendrogram branches indicate the distance between species in the functional trait space. Using this functional dendrogram and presence-absence matrix of bird species in each community, we calculated community level pairwise dissimilarity in functional space. The Sørensen functional dissimilarity here represents the total functional beta diversity (FBeta) which can be decomposed into Simpson dissimilarity representing the turnover component (FBeta-turn) and the difference between the Sorenson and Simpson which represents the nestedness component (FBeta-nest) of functional trait groups.

Statistical analysis

Habitat states of mopane

We defined the habitat states as groups distinguished on the basis of dissimilarity in relative values of habitat attributes. Before the determination of groups, we selected the eight habitat attributes –DBH, SD, SD-small, BA, GC, SDH, TR-div and GC-div. Since the attributes had different units from each other, we standardized and scaled

them by dividing the value of each attribute by its sum. The high number of variables increase dimensionality leading to heterogeneity between clusters. Therefore, we performed dimension reduction by removing variables with poor contribution to multidimensional space. We did this by subjecting all attributes to PCA and examining the PCA result using the circle of equilibrium contribution in the PCA biplot. The radius of this circle represents the length of the vector that would have equal contribution in the multidimensional PCA space (Legendre *et al.*, 1988; Borcard *et al.*, 2011). We dropped four attributes, SD-small, GC, TR-div and GC-div, as their vector lengths were shorter than the equilibrium circle radius.

Using the remaining attributes, DBH, SD, BA and SDH, we calculated the Bray-Curtis dissimilarity index and subjected it to hierarchical clustering using the Ward method which clusters plots on the basis of the minimum increase in the total within cluster variance (Ward, 1963; Legendre *et al.*, 1988; Borcard *et al.*, 2011).

To decide the appropriate number of clusters more objectively, the majority rule method following Charrad et al. (2014) was used, where, the dissimilarity matrix was subjected to 27 indexes of cluster validity; the optimum number of clusters is then the number suggested by majority of indexes. Further, we tested the stability of the selected clusters by bootstrap resampling using 10,000 iterations and computing the within cluster similarity using Jaccard similarity coefficient. When Jaccard coefficient value was >0.6, the cluster was considered stable.

Effect of disturbance on the woodland habitat

To investigate the effect of disturbance on habitat structure and composition, we first examined how habitat groups are related to the type (elephant or human) and intensity of disturbance for which we used the tree regression models. Further, to examine the effect of disturbances on the individual habitat attributes, we developed candidate models for each of the eight attributes with the two disturbance and the three orthogonal indirect impact variables as predictors in linear additive combination.

Effect of disturbances and habitat attributes on diversity, species and traits of birds

We tested the effects of disturbance variables and habitat attributes together on diversity parameters, species incidence, and functional traits using 120 sampling units clustered within 40 grids. We modelled the three species diversity (species richness, turnover, and nestedness) and three functional diversity parameters (functional diversity, turnover, and nestedness) in response to disturbance variables (including the indirect impact indicators; n=5) and habitat attributes (n=7) in linear additive combinations. We excluded GC-div as, during the preliminary examination of the variables, it did not show a significant effect on any of the diversity parameters. We developed candidate model for each diversity parameter and used model selection (described below) to identify the best set of predictors among the disturbance variables and habitat attributes.

In addition, to identify the species and species traits that were affected by disturbance or habitat variation, we modelled the presence-absence of species and the community weighted mean of each trait with disturbance variables and habitat attributes as predictors. To assess individual species, we modelled occurrence of species sighted > 5 times (n=38) in a generalized linear mixed effects model with binomial errors. These individual species occurrence single visit models do not take in to account co-occurrence and heterogeneity in detection and therefore should be inferred with caution.

Model identification, selection and validation

Where the response variables were a count (species richness) the generalized model with Poisson errors were used. The model with binomial errors was employed for occurrences of species. The sampling plots in the present study were spatially structured and clustered within sites. To accommodate the sources of correlation due to the clustered sampling, we used the mixed effects modeling framework. In the mixed model, we specified the site that a plot is nested in as a random factor. The model selection was first done manually by backward selection. After

identifying the simplified model, model validation was done for each candidate model to check for assumptions of normality of residuals and homogeneity of variance. To reduce residual heteroscedasticity, the variables were natural logarithm transformed (Y + 1) if the model residuals did not fulfil the normality and homogeneity of variance criteria. The full model construction, simplification, and selection were again done using the automated model selection on transformed variables. In the automated model selection, 100 models are generated by all possible additive combinations of predictor variables and are compared using the Akaike Information Criterion (AIC). The lower AIC values indicate higher parsimony in the model and the model with lowest AIC is selected as the best model. The results of automated and manually selected models were identical and so the outcome of only automated model selection are described in the results. To quantify the amount of variance explained by the selected model of a habitat attribute, we computed the marginal (variance explained by fixed effects) and conditional (variance accounted by the fixed and main effects together) R^2.

Packages, function and R code

For clustering, we used the *hclust* from the *cluster* package (Maechler, 2010). We determined the adequate number of clusters using function *NBClust* in the NBClust (Charrad *et al.*, 2014) and tested the stability of clusters by the *clusterboot* function in the *fpc* (Hennig, 2013). For tree-based regression, we used *partykit* (Hothorn *et al.*, 2016). We used the vegan package (Oksanen, 2013) to compute species richness, *adespatial* (Dray *et al.*, 2016) to measure the turnover and nestedness components of species beta diversity and *CommEcol* package (Melo, 2016) for functional beta diversities. For functional alpha diversity we modified the codes and followed instructions by Swenson (2014). To fit the mixed models we used the lme4 package (Bates *et al.*, 2017). For manual model selection and model validation we used codes, and instructions provided in Zuur et al. (2009), for automated selection of mixed models we used *glmulti* package (Calcagno *et al.*, 2010), and to compute the model R^2 (marginal and conditional) we used *piecewiseSEM* package (Lefcheck, 2016).

Results

Habitat states of the mopane woodlands

For the selected four habitat attributes, DBH, SD, BA, and SDH, the first two PCA axes accounted for ~87% of the variance. In the majority rule method based determination of hierarchical clusters, nine indexes of the total 27 suggested three as the optimum number of partition (Figure 2a). The Jaccard similarity coefficient for clusters was > 0.65. Groups based on the clusters are referred as S1, S2, and S3 here onwards (Figure 2b).

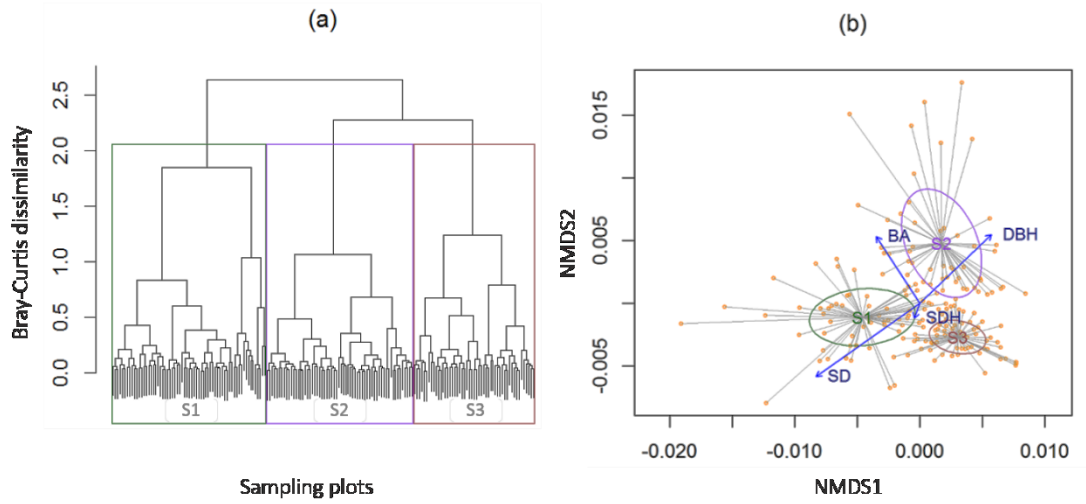


Figure 2: Based on the four habitat attributes (DBH=quadratic mean diameter, SD=Stand density, BA=Basal area and SDH=structural diversity), the sampling plots in the mopane woodlands of Zambia can be classified into three hierarchical clusters (a) representing three distinct habitat groups: S1, S2, and S3 (b). The plots in S1 have the highest Stand density and structural diversity, S2, the highest stem size (DBH) but lowest stand density (SD) and S3, have the lowest basal area (BA) and structural diversity (SDH).

Among the groups, S1 can be characterized by highest stand density and structural diversity, S2 by the highest DBH, but lowest stand density, and the S3 by the lowest DBH, basal area and structural diversity (Figure 3). The DBH (mean DBH) of S1 was lower than S2 but higher than S3, although the difference between DBH of S1 and S3 was not significant ($p>0.1$). Stand density and structural diversity significantly differed between all pairs of groups. The basal area differed significantly between S1 and S3 but not between S1 and S2. Hence, although S1 and S3 did not have

significantly different DBH, they varied in terms of basal area while S1 and S2 having different DBH did not differ in basal area (Table 2).

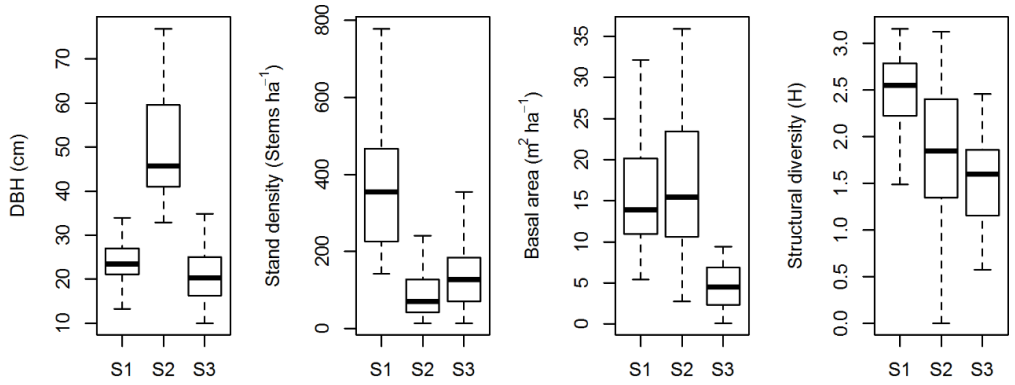


Figure 3: Comparison of selected habitat attributes between the habitat groups (S1, S2 and S3) determined by hierarchical clustering. S1 had highest stand density and structural diversity, S2 had the highest mean DBH and lowest stand density and S3 had the lowest basal area and structural diversity.

Table 2: The mean values of the habitat attributes with standard errors (±) in each of the habitat states along with the overall mean. The alphabets (a-c) indicate significantly ($p<0.05$) different groups. The R^2 represents the amount of variation explained by the habitat groups and are computed fitting the main effects ANOVA.

Structural states	DBH	SD	BA	SDH
Overall mean	31.24 (± 1.36)	204.41 (± 12.36)	12.18 (± 0.65)	1.89 (± 0.05)
S1	23. 9 (± 1.4)[a]	370.6 (± 14.1)[a]	15.6 (± 0.83)[a]	2.4 (± 0.08)[a]
S2	53.3 (± 1.6)[b]	92.1 (± 15.5)[b]	17.6 (± 0.9) [a]	1.81 (± 0.09)[b]
S3	20.8 (± 1.4)[a]	134.1 (± 13.7)[c]	4.64 (± 0.81)[b]	1.45 (± 0.08)[c]
R^2	0.60	0.55	0.44	0.31

[a-c] indicate that group means were not significantly different between the pairs.

Relationship between disturbances and habitat groups

Amongst the habitat groups, the intensity of HI was closer to the average (15.18%) in S1, lowest in S2 and highest in S3. The WI, on the other hand, was more prominent in S2 and significantly lower in S1 and S3. Higher HI intensities (>44%) were associated with S3 while WI (>11%) was associated with S2 (Figure 4).

In the tree classification models, we found that most plots with ≥44 % HI and <11% of WI were classified into S3 with an error rate less than 17%. In addition, a majority

of plots showing ≥11 % WI were classified as S2 with the error rate of 30%. The remaining plots (HI<44% and WI<11%) showed high variability (error rate 49%) with the majority of them being grouped into S1. All the nodes in the classification tree were significant ($p<0.01$). Here, we rename the groups S1, S2, and S3 as Medium human-disturbance, Elephant, and Human plots.

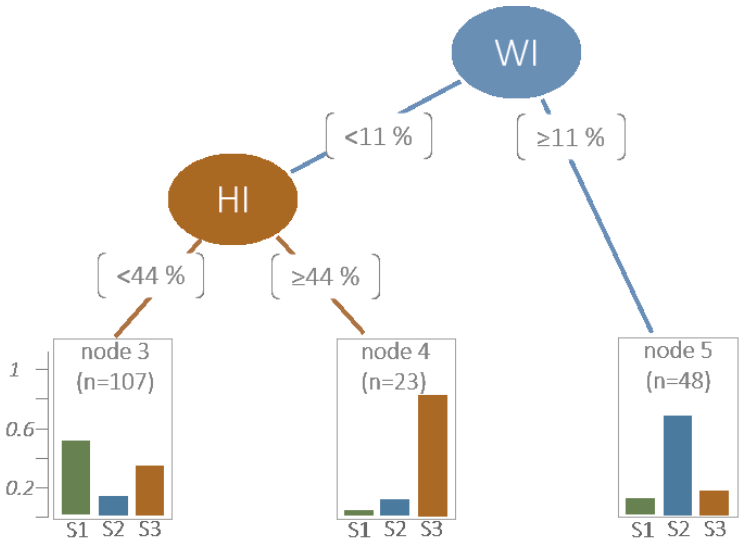


Figure 4: Tree based classification model indicates that plots with higher elephant disturbance (WI) are more likely to be classified in S3 while plots with higher human disturbance (HI) are more likely to be in S2 although considerable human disturbance is also present in S1.

Effect of disturbances on individual habitat attributes

Both HI and WI had a negative effect on stand density, but they affected the other habitat attributes differently (Figure 5a). WI was associated with an increase in DBH and decrease in structural diversity, but no change in the basal area. HI was related to decrease in basal area, increase in density of small stems (<10 cm DBH) and percentage of ground cover, but no change in DBH. Below we provide details about their effects. The measures of DBH, stand density, basal area and small-stems were log-transformed. Hereafter DBH, stand density, basal area, and small-stems imply their log transformed values.

DBH increased with WI (percentage deviation from the mean ± standard error, 4.7 ± 1.2 %), and decreased sharply with proximity to populated areas (-49 ± 18 %). WI

did not have any effect on the basal area as it was not selected in the best fit model. Basal area declined significantly with increase in HI (-13.3 ± 4 %) and declined albeit non-significantly in response to populated, remote and protected areas. Although WI and HI were associated with the DBH and basal area differently, they both had a significantly negative effect on stand density (WI: -7.1 ± 1.5 %; HI: - 4 ± 1.3 %). The effect of WI was larger than HI (1.7 %). While HI was associated with decline in the density of larger stems, it affected the density of smaller stems positively (18 ± 7 %). In addition, small stems decreased but non-significantly with proximity to protected, populated and remote areas. Ground cover showed an identical pattern of response, increasing with HI (6 ± 3 %) and decreasing in populated, protected and remote areas. Lastly, the vegetation diversity attributes of the habitat (TR-div and GC-div) did not show any significant association with any of the disturbance variables.

Among the habitat attribute models (n=8), the marginal R^2 ranged from 0.03 to 0.24 (Figure 5b). That of DBH, SDN and BA models were 0.25, 0.24 and 0.1 respectively. The conditional R2 was more than >0.25 for all models.

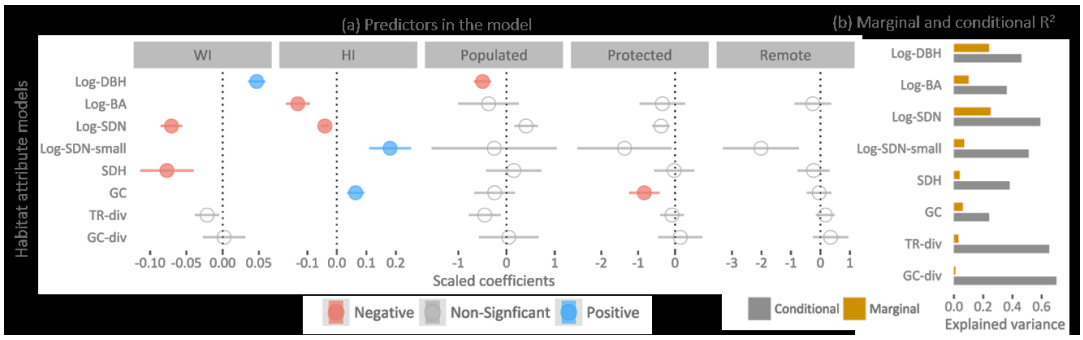


Figure 5: The scaled coefficients (proportion of deviance from the intercept) of predictor variables selected in the best model for each habitat attribute with horizontal error bars as standard error show the negative effects of elephant (WI) and human disturbance (HI) on stand density, their dissimilar effects on other habitat attributes.

Effect of disturbance on species alpha and beta diversity of birds

During the course of this study, we observed a total of 132 birds species with mean plot level species richness of 7.4 (± 0.06) and beta diversity of 124.6 (± 0.07). Based on Hill number rarefaction and extrapolation, the asymptotic species richness estimate was 180 (± 18) species for the whole study area. The overall sample completeness was 0.95 indicating that we encountered majority of species found in the study area. The estimated asymptotic species richness, 136 (± 18), 97 (± 17) and 110 (± 15) varied between the habitat groups, *Medium human-disturbance* (S1), *Elephant* (S2) and *Human* (S3) respectively (Figure 6).

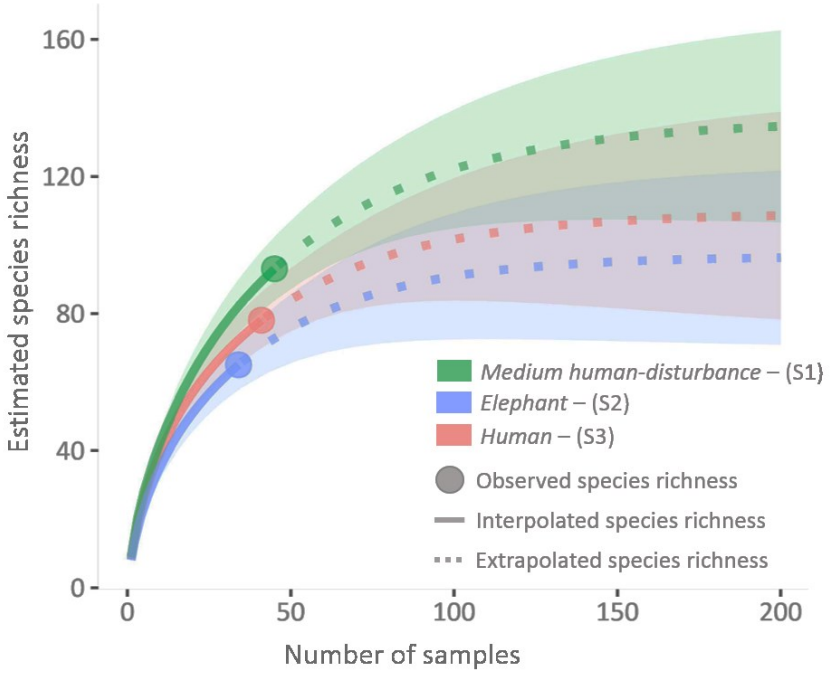


Figure 6: Rarefied and extrapolated sample and incidence based species richness estimate with 95 % confidence intervals indicating higher estimated richness in areas classified as S1-average, followed by richness in S3-human and S3-elephant.

The mean species richness (log scale) decreased by 5.5 % (± 2.3) and 4.3 (± 2.1) with each unit increase in WI and HI respectively, and increased by 7.8 (± 2) with TR-div (Figure 7). Further, WI was also associated with decrease in the turnover component of beta diversity (- 6.1 ± 2.4%), while HI had no significant effect. The other

predictors (Populated, Protected, and Remote) in the model for the turnover component had non-significant effects. The nestedness component did not show a significant response to any of the disturbance variables or habitat attributes (HI, Populated, Protected, and Remote).

Among the three species diversity models, the model for species richness had the highest marginal R^2 at 0.17, while those of turnover and nestedness components of beta diversity were low at 0.07 and 0.03 respectively. Conditional R^2 was 0.57, 0.37, and 0.04 for species richness and turnover and nestedness models respectively.

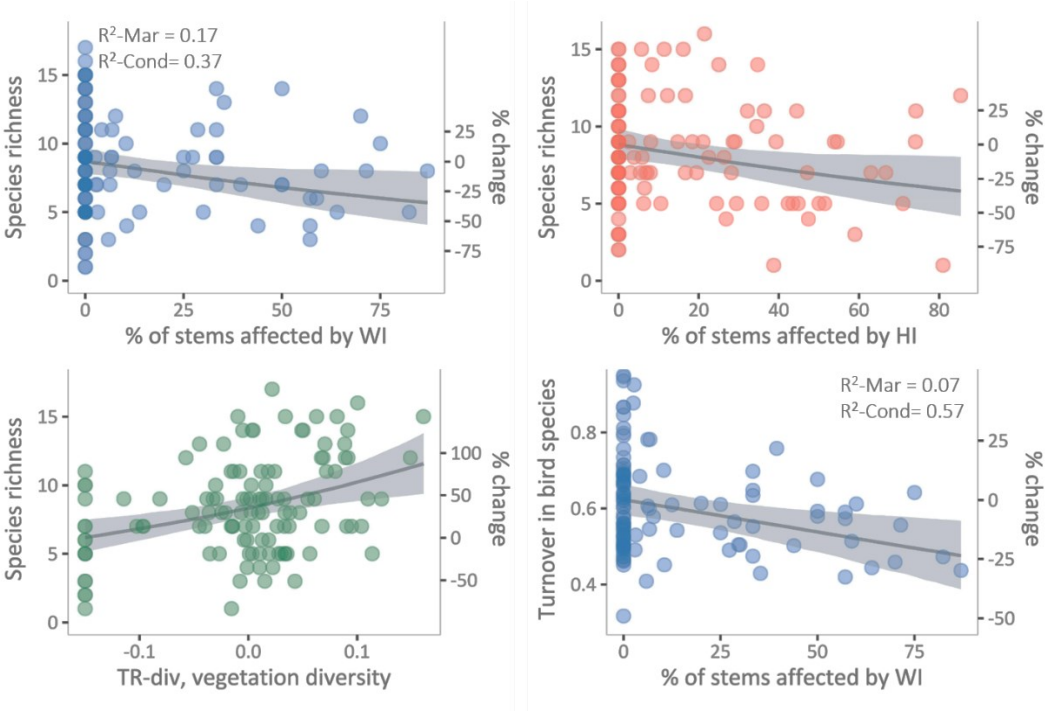


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Figure 7: Species richness of birds decreased with elephant (WI) and human (HI) disturbance and increased with TR-div (TR-div was derived from the PCA 2 axis which was correlated with alpha and beta diversity of trees). In areas affected by the elephant disturbance, the turnover component of beta diversity of bird communities reduced. In the above plot, the circles indicate observed diversity, lines represent the best fit and shaded areas indicate the 95% CI of the fitted line estimated by bootstrapping.

Effect of disturbance on functional alpha and beta diversity

MFD (mean functional distance) declined with HI (- 4.2 ± 1.8%), increased with TR-div (7.6 ± 1.8%). The other predictors in the model, had non-significant effects (Figure 8). WI was not included in the model for MFD. In the model of the turnover component of functional beta diversity (FBeta-turn), WI showed negative effect, and other predictors, Populated, Protected, and Remote had non-significant effects. The nestedness component of functional beta diversity (FBeta-nest) increased with HI (0.1 ± 0.04) and decreased with Remote (-1.16 ± 0.5) and ground cover, GC (-0.11 ± 0.04). Basal area and Protected were the other predictors in the nestedness model, but with non-significant effects.

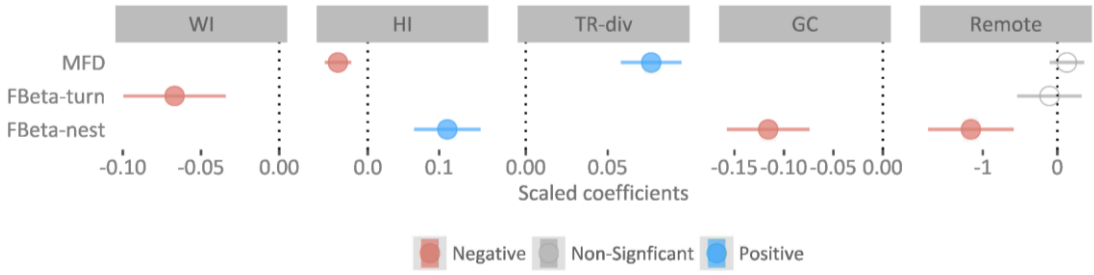
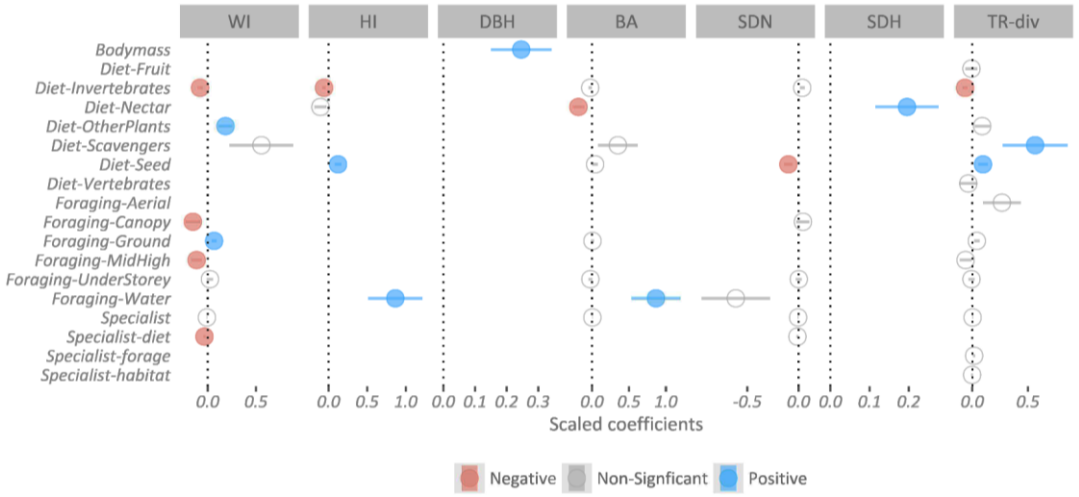


Figure 8: The result of mixed effects models show different effects of WI and HI on functional diversity (MFD) and composition. HI reduced functional diversity, but WI did not. Instead, WI was associated with reductions in the functional dissimilarity (FB-turn). The circles represent scaled coefficients (proportion of deviance from the intercept), horizontal lines indicate the standard error, and colours denote direction of the relationship between the disturbance and habitat variables (only the significant predictors are shown) and functional diversity parameters.

Which species and traits are affected by disturbances?

The trait models indicated that in invertebrate-feeders, canopy and mid-story foragers, and diet specialists had a negative, while ground foragers and plant-feeders showed a positive relationship with WI. In response to HI, seed-eaters and species foraging near water bodies increased, while invertebrate-feeders declined (Figure 9). In addition, species of higher body mass increased with DBH, nectar-feeders declined with basal area and increased with structural diversity, seed eaters declined with stand density and increased with the beta diversity of plants.

The trait results were further corroborated by the results from the species incidence models which showed that increasing species in WI mainly consisted plant feeders and ground foragers such as *Agapornis lilianae* and *Stigmatopelia senegalensis*, while decreasing species comprised of invertebrate feeding (*Batis molitor*), canopy or mid-high foragers or highly dominant seed preferring non-woodland species like *Quelea quelea* Figure 10). In HI areas, likewise, invertebrate feeders such as *Batis molitor* and *Prinia subflava* declined. Further, more species declined in WI than HI. Majority of species showed a positive association with basal area and vegetation diversity.



10 *Figure 9: The community weighted mean functional trait models show that invertebrates feeding species declined with both disturbances. In addition, plant feeders and ground foragers increased in HI, while canopy and mid-high storey foragers declined. Further, seed eaters and foragers near water bodies increased in HI.*

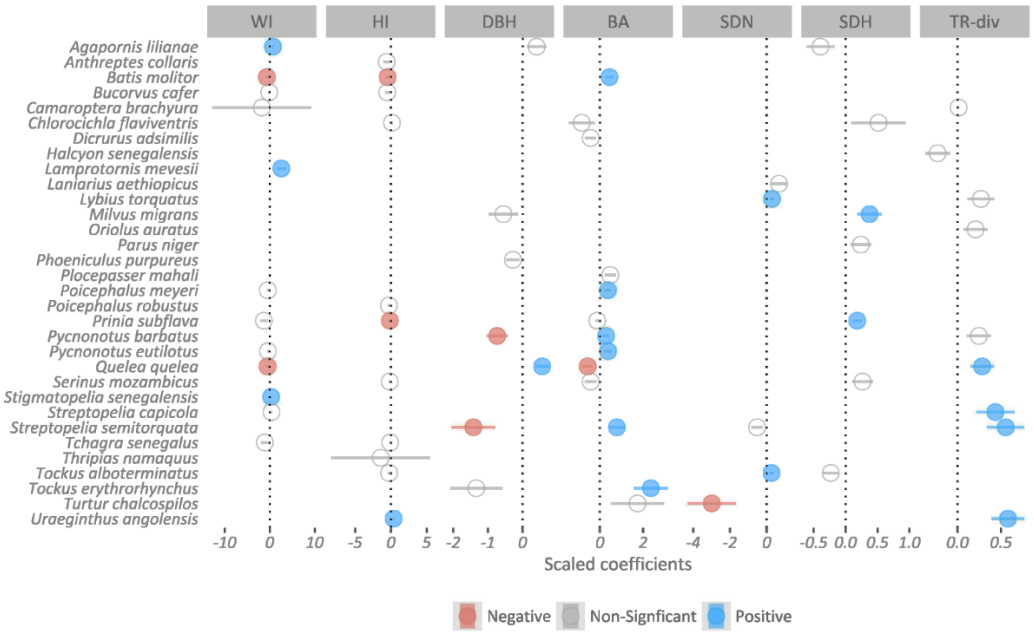


Figure 10: The species incidence models identify the species associated with disturbance and habitat variables. Species such as Stigmatopelia senegalensis and Agapornis lilianae, mainly plant feeders and ground foragers increased in WI, while insect feeders such as Batis molitor decreased in WI and HI. Areas with higher basal area (BA) and beta diversity of plants (FloBeta) showed increase in incidence of majority of species.

Discussion

In this study, we showed that humans and elephants modify the structure of mopane woodlands differently possibly due to the differences in ways in which they exploit the habitat. We also showed that across the mopane landscape in Zambia, mopane woodlands exist in three dominant forms which are related to the type and intensity of disturbance– Average-disturbance, Elephant, and Humans. As elephant and humans structure mopane habitats differently they impose dissimilar habitat filters which organize ecological communities in different ways. Our study showed that both humans and elephants reduce the species richness of bird communities. However, we also demonstrated that the disturbances affect the species composition and functional diversity differently. Bird communities in elephant affected areas become more similar to each other in species as well as functional trait compositions with no reduction in functional diversity. In contrast, in response to human disturbance, bird communities undergo reductions in functional diversity but do not experience any change in species and functional compositions.

Below we discuss our findings in relation to the research questions we asked in this study and compare our findings with other relevant studies.

What are the major structural forms of mopane woodlands? Are they related to human and elephant disturbance?

The structure of savanna woodlands is controlled by the combination of bottom-up – water and soil nutrients - and top-down factors such as disturbances by humans, elephants, and fire (Langevelde *et al.*, 2003; Sankaran *et al.*, 2005; Makhado *et al.*, 2014; Hempson *et al.*, 2015). Within the boundaries set by the abiotic bottom-up factors, the top-down controls alter the woodland attributes: tree density, basal area and composition of vegetation, and maintain the woodland in to different structural forms (Bond, 2008; Gandiwa *et al.*, 2009; Kohi *et al.*, 2011; Mapaure *et al.*, 2011;

Ferguson, 2014). Bond & Keeley (2005) showed that fire and herbivory can have similar effects on vegetation. However, Andela et al. (2017) comparing multiple satellite datasets demonstrated large decreases in fire activity in tropical savannas mainly due to the increasing human influence. Based on this, we can speculate if tree removal by humans can play the role of fire and have similar effects as that of herbivory. We evaluated the hypothesis that if humans and elephants have dissimilar effects, the mopane woodlands across our study region can be classified into distinct groups based on habitat attributes and these groups would correlate with the type (human or elephant) and intensity of disturbance (% of affected stems). We found that variation in the mopane woodland is mainly due to differences in the structural attributes. We showed that on the basis of the four structural attributes –DBH, stand density, basal area, and structural diversity, the mopane woodlands can be classified into three significantly distinct structural forms. Our study further revealed that among these structural forms, *Average (S1)* corresponds to low disturbance by both, large-herbivores (~11%) and humans (<44%), *S2 - Elephant* with large-herbivores, mainly elephants (>11%), and *S3-human* with human disturbance (>44%). With this, we show that elephants and humans can lead to altered structural states of the woodland. Hence, our analysis suggests that humans and elephant as top-down factors are important determinants of structural patterns in the mopane woodlands of Zambia. Assuming that fire and elephants have similar effects on vegetation as suggested by Bond & Keeley (2005), we conclude that the effects of humans may not be interchangeable with elephants or fire.

How human and elephant disturbance affects habitat attributes of the mopane woodland?

Reduction in stand density in response to elephant impact (7.1 ± 1.5%) was 1.7 times higher than the human impact (4.1 ± 1.3%). This is comparable to a recent spatial assessment of treefall rates by Mograbi et al. (2017) in *Combretum-Acacia* woodlands. Mograbi et al. (2017) compared the rates of treefall between human impacted,

elephant impacted and control sites using Light Detection and Ranging technology and found human-mediated treefall to be 3-5% ha^{-1} and elephant-mediated treefall to be 7% ha^{-1}, both closer to the field-based estimates of this study. Similar study by (Asner *et al.*, 2012) in Kruger National Park (KNP) noted treefall rates of 6% by elephants.

Basal area (which is correlated with woody-biomass) in response to elephant disturbance in this study was not significantly different than the areas with no elephant disturbance. Holdo et al. (2009) using their spatial simulation model predicted no change in woody biomass if the elephant densities were maintained below 0.15 km^{-1}. Ben-Shahar (1996) compared the effect of elephant densities on biomass and also suggested no reduction in biomass if the elephant densities are below 0.15 km^{-1}. In our study area, the average elephant density in 2015 was estimated at 0.44 km^{-1} (Luangwa ecosystem=0.43 km^{-1}, Lower Zambezi Valley=0.45 km^{-1}; DNPW 2016), above the threshold suggested by Holdo et al. (2009). Yet, we did not find a significant change in biomass compared to areas that had low elephant impacts. There can be three reasons for this: (i) areas where elephant impact was absent, there could be other disturbances controlling the woody biomass, (ii) elephant impacted areas maintain total wood biomass through large trees, or (iii) the elephant numbers are not reflective of the sites in this study.

We found that the DBH increased with the intensity of elephant disturbance while the basal area, vegetation diversity and ground cover did not change significantly. This matches with the findings of O'Connor & Page (2014), who assessed the effect of increasing elephant densities between 1997 and 2010 after elephants were reintroduced in the 1990s in the Limpopo Province of South Africa. They found no significant change in vegetation diversity and composition in the mopane woodlands, reduction in stem densities, and increase in stem basal area (equivalent to the quadratic DBH which we used in this study) of *C. mopane* stems in non-riverine habitats.

Elephants are known to knock down trees of larger size classes up to 5 m (Vijver *et al.*, 1999; Asner *et al.*, 2012) and maintain them as mopane morphs (Vijver *et al.*, 1999; Smallie *et al.*, 2000). Vijver et al. (1999) demonstrated this, in their temporal comparison of effects of elephant and fire, by showing an increase in density of stems in the 1-5 m height class and a strong decline in density of stems above 5 m height in the deciduous savanna. They also noted a decline in density of stems below 1 m height. Their <5 m height-class range is equivalent to small stems (<10 cm DBH) in this study. Small stems in this study did not increase significantly with elephant disturbance. However, Vijver et al. (1999) distinguished between small stems (height = 1-5 m) and very small stems (height <1m) which we did not. Thus we did not differentiate between the effects of elephants on very small stems – possibly regenerating stems, and small stems-primarily elephant stunted stems.

Utilization by large herbivores is known to be responsible for changes in the structural composition of the mopane woodland (Smallie *et al.*, 2000; R. A. Makhado *et al.*, 2014). By debarking, coppicing, pollarding and stunting mopane stems, they tend to transform the woodland into patches of low biomass shrubby system which occur along with patches of high biomass big sized stems (Smallie *et al.*, 2000). Although there may be occasional debarking on the bigger stems (>4m height, >20cm DBH), the main disturbance by elephants, however, is the pollarding and coppicing of stems for browse (Anderson *et al.*, 1974; Smallie *et al.*, 2000; Ferguson, 2014). Most of the browsing is known to occur on the stems of <4 m height with previously utilized and coppiced stems of <2 m being preferred as they consist of significantly more branches providing additional, easily accessible and better quality browse (Smallie *et al.*, 2000). Since the browsers prefer to use stems of a certain size and reutilize the mopane patches they degraded before, the stems which escape their utility threshold generally attain bigger size and higher basal area, this counter balances the biomass lost due to the shrubby state created by browsers. Ben-Shahar (1996) highlighted that, except in cases of high densities, elephant utilization may not result in drastic loss of biomass. The mopane woodlands in most protected

areas devoid of human disturbance, and consisting of elephants and other big browsers may, therefore, have a different structural composition than the woodlands in areas with human disturbance or with no or little disturbance. On the basis our study, we find an indirect evidence of this process, we show that the *mopane* woodland in more elephant (or broadly, big browser) dominant landscape can be characterized by a significantly low stand density, but with a considerably high DBH, and with basal area (or biomass) not significantly different from the undisturbed woodland.

In human dominated land use, the mopane woodlands are subjected to different processes. While the elephants largely utilize the mopane stems for browse and selectively revisit and reuse the previously utilized mopane patches, the human use of the woodland is largely driven by the need of timber and fuelwood especially for charcoal production leading to upsurge in selective logging of stems of preferably bigger size (Hosier, 1993; Ndegwa *et al.*, 2016; Woollen *et al.*, 2016). As shown in a number of studies in the mopane and other woodlands closely related to the mopane (Backéus *et al.*, 2006; Fontodji *et al.*, 2011; Ndegwa *et al.*, 2016; Kiruki *et al.*, 2017), the selective logging more likely results in reduction of stand density and also the overall basal area. In this study, we confirm this widely observed trend of the impact of human disturbance.

Why there is a difference between humans and elephant effects?

Elephants, like fire, suppress regeneration and prevent saplings from escaping the grass layer. The recruitment depends on rare opportunities(Bond, 2008). Once the saplings escape the grass layer (1 m), they have to also escape the browse trap (1-5 m; Staver & Bond 2014). Beyond these thresholds, the trees are less vulnerable to elephant damage. However, they may still be susceptible to fire damage (Bond *et al.*, 2005). Assuming that fire occurrences and intensities have reduced (Archibald *et al.*, 2012; Andela *et al.*, 2017), these escaped adult trees can persist for decades (Bond, 2008). Also as the overall number of trees are reduced by elephants, the escaped

trees face reduced competition and can grow larger in size (Bond, 2008; Staver *et al.*, 2014). The woody biomass lost due to the removal of trees can thus be counterbalanced by the accumulated woody-biomass in the large trees. This is the most plausible explanation for no change in woody biomass in the elephant degraded plots in our study. In high elephant densities, beyond a certain threshold, the chance of escape will be strongly reduced and even mature trees can be vulnerable to damage due to a large population of elephants. In human dominated regions of mopane, selective logging of large stems driven by the need for charcoal, fuelwood, and timber does not have any large stem survivors in areas which are accessible to humans (Mograbi *et al.*, 2017). Hence at the landscape level, the human affected areas are likely to undergo a decline in woody biomass leaving behind small undesired and coppicing stems. Therefore, humans and elephants, due to the different ways in which they interact with the woodland, have dissimilar effects on the structural attribute of the woodland which may lead to altered structural states of the woodland.

How does disturbance due to humans and elephants affect species diversity of birds?

The biodiversity of the dynamic African savanna woodlands is unique and important, yet this study is among only a few assessments of how disturbance affects biodiversity in these ecosystems. We found human and elephant disturbance had a negative effect on species richness and dissimilar effects on species composition of bird communities. Our finding of negative consequences of human disturbance matches with the narratives of spatial-comparison based global (Murphy *et al.*, 2014; Newbold *et al.*, 2015) and the African savanna syntheses (Newbold *et al.*, 2017) that local species richness reduces in response to increasing land use pressures. Also, our evidence about negative effects of elephant disturbance on species richness of birds corroborates findings of Cumming et al. (1997) and rebuts that of Herremans (1995). Cumming et al. (1997) compared intact and elephant damaged sites, whereas Herremans (1995) compared the intensity of

elephant damage based on the number of impacted trees. The study by Herremans (1995) lacked non-impacted sites and also did not consider elephant impact in relation to tree density. Therefore, their study does not truly represent a true intensity gradient of elephant impacts. Our study included areas that did not have any elephant effect, thus it aligns closer to Cumming et al. (1997) and reaffirms that species richness is lost in response to elephant damage. Also, average elephant density in our case was about ~ 0.43 km-1, closer to the density (0.5 km-1) observed in Cumming et al. (1997).

In a woodland habitat, the total woody biomass represents the main resource that the dependent faunal species exploit for food and nesting (e.g. birds, in case of our study). This resource is distributed among several trees in a plot. Trees of different size classes (DBH or height) and of different species increase structural and biotic heterogeneity, in other words, provide "habitat heterogeneity" which increases niche partitioning and supports more biodiversity than a more homogenous habitat would have (Tews *et al.*, 2004; Emmons, 2011). In this study, human and elephant disturbances reduced species richness. As these disturbances were also associated with reduction in tree densities, we claim that loss of species richness in our study was mainly due to reduction in resources underpinned through tree densities. We described in the earlier sections that the total basal area i.e. total woody biomass did not change and DBH increased in case of elephant disturbance. The basal area and DBH were not significantly related to species richness of birds. This demonstrates that tree density is more important than the total woody biomass or tree size for species richness of birds. Skowno & Bond (2003), comparing bird communities in response to vegetation structure and composition in savannas of South Africa, noted that vegetation structure is more important than floristic composition. We did not observe this pattern. We note that floristic composition is as important as tree density as species richness of birds increased with alpha and beta diversity of trees in our study (Vegetation PCA axis 1, TR-div).

Bird communities in response to elephant disturbance underwent taxonomic homogenization as they reduced in spatial turnover and increased in nestedness. We showed that structural diversity reduced in response to elephant disturbance, mainly due to the elimination of mid-strata (1-5 m height or 10-20 cm DBH). Invoking the "Habitat heterogeneity theory" (Tews *et al.*, 2004), we speculate that the reduction in structural heterogeneity would have resulted in a loss of the locally rare or non-ubiquitous species. This (common) *winner*-(non-ubiquitous) *loser* species replacement (McKinney *et al.*, 1999; Tabarelli *et al.*, 2012) is the most plausible explanation (Socolar *et al.*, 2016) for the reduction in beta diversity of bird communities in response to elephant disturbance.

Birds in response to human disturbance did not experience any significant turnover or nestedness, a typical pattern of communities undergoing subtraction through stochastic competitive exclusion (Segre *et al.*, 2014). However, we suspect that our inference may have confounded the effects of immigration. It is possible that bird communities in response to human disturbance underwent a reduction in beta diversity, but those losses were counterbalanced by spill-over from the neighbouring farmland bird communities.

How does disturbance due to humans and elephants affect functional diversity of birds?

Flynn et al. (2009) suggested four possible trajectories of functional and species diversity response: low functional redundancy (rate of species and functional diversity decline is identical), high functional redundancy (species diversity declines, but functional diversity remains constant), functionally redundant species lost first (rate of functional diversity decline is lower than species richness), and functionally unique species lost first (rate of functional diversity decline is higher than species richness). In this study, human disturbance had identically negative effects on functional diversity (- 4.2 %) and species richness (- 4.3%), validating the low functional redundancy hypothesis. Elephant disturbance reduced species

richness and did not have any significant effect on functional diversity, hence, supporting the high functional redundancy hypothesis of Flynn et al. (2009). In addition, our finding of the negative effects of human-led habitat modification on species and functional diversity is consistent with the syntheses of Flynn et al. (2009) and Luck et al. (2013).

Further, the variability in functional composition (turnover) of communities in elephant disturbed areas reduced. This indicates, that although the functional diversity of bird communities is maintained, the communities became functionally more homogenous at the landscape scale in response to elephant disturbance. In the earlier section, we discussed that decline in species richness may be linked to reduction in tree density. Drawing a similar corollary, here we propose that functional diversity patterns of birds are congruent with the patterns of basal area response to disturbance. The functional diversity and basal area, both reduced in response human disturbance and did not change significantly in response to the elephant disturbance. Thus reduction in functional diversity of birds may be explained by the reduction of the overall resource, the total woody biomass in the landscape. In other words, assuming that the woody biomass represents the amount of available niche in the woodland habitat, the functional diversity loss can be explained by the reduction and convergence of this niche space. This inference matches with other bird-diversity and habitat-structure studies (Hidasi-Neto *et al.*, 2012; Sitters *et al.*, 2016). Most functional diversity – productivity understanding is based on plant communities under experimental conditions (Cardinale *et al.*, 2011). With this we provide empirical evidence of the positive relationship between woody-biomass and functional diversity of birds in the mopane woodlands. To our knowledge, there are no known studies that have assessed changes in functional diversity of communities in response to disturbance or land use activities in the African savanna woodlands. Thus, this the first analysis to show that elephant and human disturbances have dissimilar effects on functional diversity and thereby may have different consequences on ecosystem functioning. Human disturbance may be

detrimental to functioning of ecosystems, while elephant disturbance may not have any immediate local effect, although the resilience of ecosystem functioning is possibly compromised due to spatial functional homogenization.

Which species and functional traits of birds are affected by humans and elephants?

We showed that birds that have diets primarily of invertebrates declined in response to both disturbances. This is a common observation across the majority of studies that have assessed the effect of land use pressures on functional traits of birds (e.g. Newbold et al. 2013; Newbold et al. 2014; Edwards et al. 2013; Tscharntke et al. 2012; Sekercioglu 2012; Luck et al. 2013). These studies also suggest negative effects of land use activities on species with larger body sizes. We did not observe any effect of disturbances on body size directly. However, body size was positively associated with tree size in our study. Human disturbance of high intensity is more likely to reduce the mean tree size and thus affect bird species of larger body sizes. The negative effect of disturbance on invertebrate-feeding traits is most possibly because of reduction of tree-bark dwelling insects in response to the declining density of trees imposing bottom-up stress on bird species (Duguay *et al.*, 2000). Further, we showed, species that forage on the canopy and mid-high strata and are diet-specialists have a negative association, while species that feed on plant matter and forage on the ground have a positive relationship with elephant disturbance. The combination of traits - foraging on the canopy and mid-high strata and diet specialization indicate towards the non-woodland species - *Quelea quelea,* which is a non-ubiquitous species and functionally redundant in the bird communities of the mopane woodlands. The plant-feeding and ground-foraging trait points towards the mopane woodland specific and locally ubiquitous species - *Agapornis lilianae* (Endemic and near threatened) and *Stigmatopelia senegalensis.* These represent the functionally unique species in the mopane woodlands. Hence, with elephant disturbance, locally rare species (functionally redundant) are lost and locally common species (functionally unique) persist, representing the typical pattern of

(common) winner- (rare) loser replacement in native assemblages (WLR; Tabarelli et al. 2012) leading to local biotic and functional homogenization. With human disturbance, seed-eaters and species foraging near water (*Uraeginthus angolensis*) showed a strong positive association. In response to human disturbance, number of locally common invertebrate-feeders (*Batis molitor* and *Prinia subflava*-HI) were replaced by fewer, but commonly occurring seed-eaters (*Uraeginthus angolensis*). However, WLR in this case does not lead to biotic homogenization as suggested by McKinney & Lockwood (1999). Being a common-common species replacement it adheres to the competitive exclusion principle we discussed in previous sections. Nevertheless, it leads to subtraction of species and functional diversity with no effect on beta diversity.

Conclusions

We conclude that humans and elephants are associated with different forms of mopane woodlands and that they affect the habitat attributes and species and functional diversity of birds differently. We showed that, in spite of the reduction in stand density, the elephant disturbance did not affect the total basal area as it was associated with an increase in average stem size. Human disturbance, on the other hand, was linked to reduced stand density and total basal area and increase in density of small stems with no change in mean stem size. Thus, as biomass is correlated to basal area, we can conclude human disturbance reduces woody biomass, while elephant disturbance does not. Further, although both disturbances reduced the species richness of birds, human disturbance was not associated with any effect on species composition of birds, while elephant disturbance was related to the decrease in the dissimilarity between communities in species compositions (biotic homogenization). Functional diversity of birds reduced with human disturbance but did not change significantly with elephant disturbance, although bird communities became functionally homogenous with elephant disturbance. In short, elephant disturbance is associated with subtractive biotic homogenization and landscape level functional homogenization with no effect on functional

diversity, while human disturbance is related to subtraction of species and functional diversity. To take the "human problem" and "elephant problem" debate forward, we state that if loss of woody biomass and functional diversity is a concern, human disturbance is "bad" and elephant disturbance is not.

Limitations of this study

As this was a space-for-time substitution, we assume that spatial patterns of the response variables in this study are manifestations of their disturbance or land use histories. However, this assumption holds validity because we sampled within one land cover – the mopane woodland. Also, we took in account the distance based variables which can affect our results such as distance from water-body, river, nearest populated area, and elevation. Notwithstanding, our results can be biased by temporal variations and detectability. This study, however, provides evidence about possible trends and patterns in the dynamic and understudied African savanna woodlands and highlights the need to carry multi-seasonal research to get a get a clearer picture of how savanna woodlands are changing in response to increasing human dominance.

Future research

1. In the human dominated areas of savanna, which comprises of most savannas, livestock grazing can interact with the effects of woody biomass removal by humans. This can further have strong interactions with fire. Future studies should focus on understanding the complex interactions between grazing, fire, humans and wild-herbivores and biodiversity.

2. Ben-Shahar (1996) in context to the mopane woodlands in Botswana and Holdo et al. (2009) in context to the Serengeti suggested an elephant density threshold of 0.15 km^{-1} beyond which elephant disturbance should lead to a decline in woody biomass. In this study, the elephant densities in the areas we surveyed surpassed this limit. Yet, we did not see any significant reduction in the plot level woody biomass. This

emphasizes that the impact thresholds may vary between regions and habitats. More studies are, therefore, necessary to identify elephant population density thresholds in different ecosystems and habitats.

3. While elephant disturbance is mainly density dependent, human disturbance is driven by more complex factors – local human densities, urban markets and physical access to woodlands (Ahrends *et al.*, 2010; Luz *et al.*, 2015; Ryan *et al.*, 2016; Mograbi *et al.*, 2017). Quantifying the top down stress imposed by different disturbance activities, and identifying relevant thresholds will help predict and project their consequences on biodiversity.

4. Taxonomic groups have heterogeneous responses to disturbance. Understanding those differences through a functional diversity framework will improve our understanding of the community assembly processes in the changing savanna woodlands. Future research should be directed towards using multiple taxonomic groups to identify species and functional diversity patterns in response to land use activities and disturbance agents in the savanna woodlands.

5. Elephant-human-fire interactions may have long disturbance-recovery cycles. Describing and quantifying the resilience of these woodland ecosystems is not in the scope of this study. However, to know the long term impacts of disturbances, understanding the role of resilience is paramount. Future research should thus also focus on long term temporal and spatial comparison of disturbances, habitat alterations and biodiversity changes.

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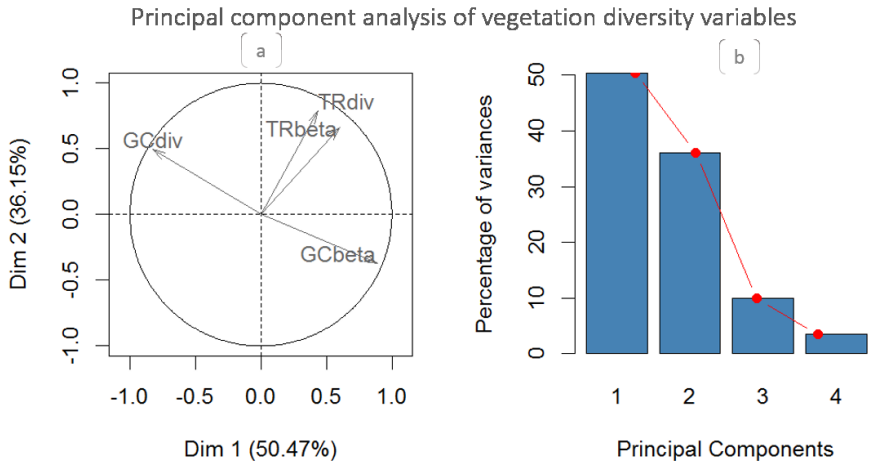
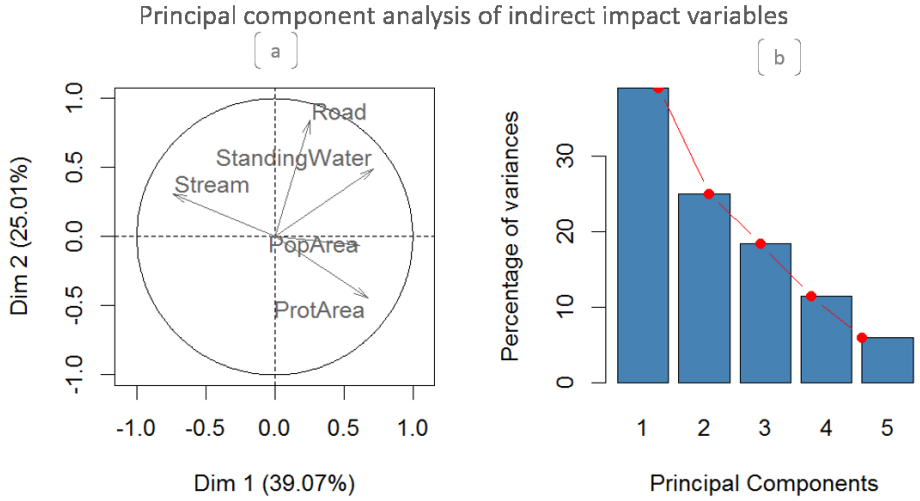
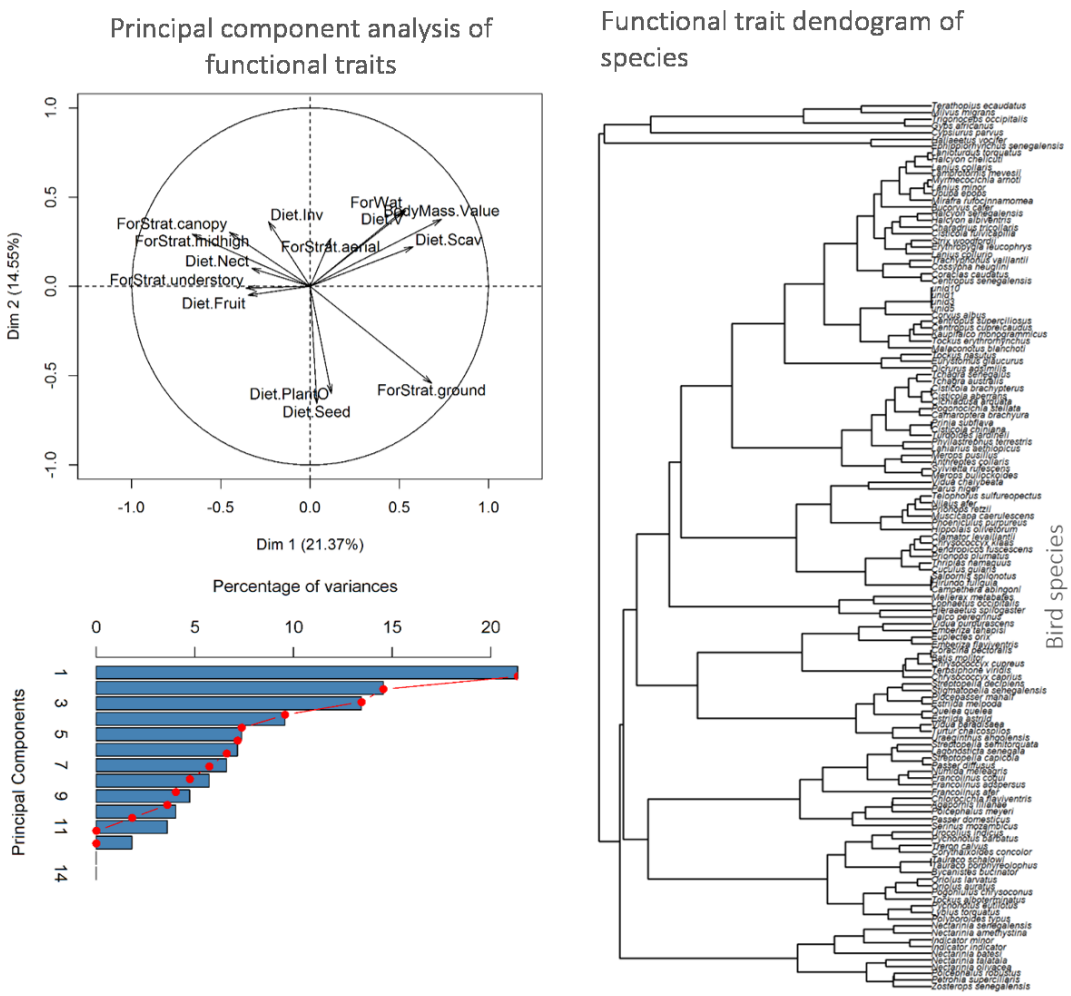
Supplementary material



SM 1 : Alpha and beta diversity of trees (TRdiv and TRbeta) were positively correlated to each other, while alpha and beta diversity of ground cover species (GCdiv and GCbeta) were negatively correlated. We used PCA to reduce the number of variables. We derived two orthogonal variables by selecting the first two PCA axes which together contributed to ~86 % variation. TR-div from the 2nd axis of the PCA and GC-div from the 1st axis.



SM 2: The five indirect effect variables in PCA were reduced to three orthogonal variables explaining 82% of total variation.



SM 3: The 14 functional traits were subjected to PCA and first 10 axes which explained 95% variation were selected for functional diversity calculation. The selected PCA axis were then subjected to hierarchical clustering using Euclidean distance and wards method. The resulting functional dendogram was used to compute functional diversity measures.

Chapter 5
General discussion

The global biodiversity-land use discourse lacks geographical breadth and underrepresents the savanna woodlands of southern Africa, a dominant savanna ecosystems in the southern hemisphere. Understanding the patterns of biodiversity response to land use in context to these woodlands at local scale was therefore the main objective of this thesis. To meet this objective, I examined the effects of the two dominant land use activities in southern Africa – charcoal production and agriculture – on alpha and beta diversities of multiple taxonomic groups. I also compared the effects of two major determinants of habitat structure in the savanna woodlands – humans and elephants– on structure of habitats and species and functional diversity of birds.

In this thesis, I provided a quantitative understanding of land use and disturbance mediated biodiversity change in these woodlands at local scales. I identified the patterns of biodiversity response, described the possible filtration and community assembly processes to explain those patterns, and explored their logical implications. Briefly, I found that land use activities and habitat disturbances lead to loss of richness by negatively affecting the majority of species, creating more *species losers than winners*. However, land use and disturbance types impose different ecological filters on different taxonomic groups producing dissimilar patterns of species compositions. Heterogeneity in effects of land use and response of different taxonomic groups therefore must be taken in to consideration for biodiversity change predictions, scenarios and conservation planning.

In this section, I first review the answers to each of the research questions I investigated and then discuss the key conclusions relating to these questions before reflecting upon their possible implications.

Answers to research questions

RQ1. How does diversity and composition of tree, mammal and beetle communities respond to charcoal production in the mopane woodlands?

In the first data chapter (Chapter 2), I showed that charcoal production mainly has disruptive effects on population size and species richness. The majority of species declined and total number of species in a community reduced as charcoal production intensified. But, there was a variability between taxonomic groups. Species richness of trees and mammals declined by about 32 % and 50 % respectively in areas with highest charcoal production intensity (intensity gradient 6), while that of ground beetles did not show a significant response (Figure 1). In addition, although both trees and mammals showed declining species richness, they differed in beta diversity response to charcoal production. The turnover component of beta diversity of trees decreased, whereas that of mammals increased. The nestedness component showed the opposite trend, increasing for trees and decreasing for mammals. This means, that as charcoal production becomes more intensive, tree communities in the region become more similar to each other. They become subsets of larger tree communities found in less disturbed areas. Mammal communities, on the other hand, become more dissimilar, and drift away from the species compositions found in low charcoal production areas. Therefore, to answer the above question, in response to increasing intensities of charcoal production, tree communities endure subtractive biotic homogenisation, mammals undergo subtractive community drift, and ground beetles show no significant variation in species richness or composition.

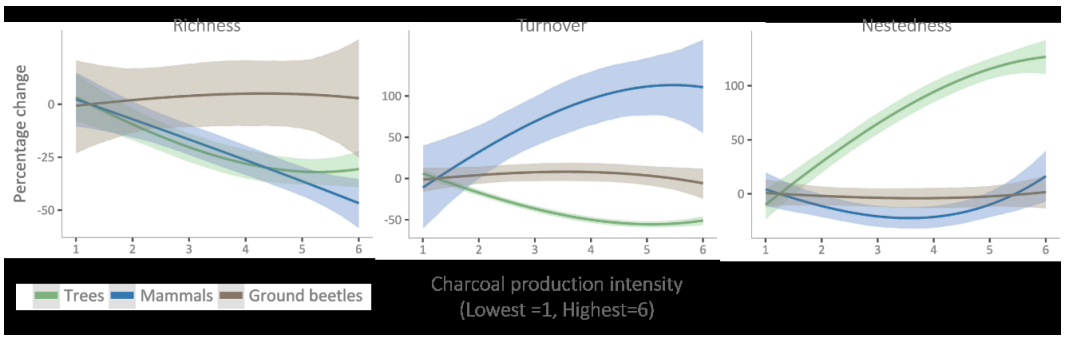


Figure 1: Among the three taxonomic groups (trees, mammals and ground beetles) the species richness of mammals and trees declined and their beta diversities (turnover and nestedness) showed varied patterns in response to the increasing charcoal intensity. Ground beetles did not significantly change in alpha or beta diversities. The charcoal intensity gradient from 1 to 6 is based on the time since charcoal production first started and peaked in the village (Intensity 1= charcoal production not started as of 2014, intensity 6=charcoal production started in 1996)

RQ2. How does fragmentation and loss of habitat due to agricultural expansion in the miombo woodlands affect tree and mammal communities?

I explored this question in the second data chapter (Chapter 3) of this thesis. The results show that as agriculture expands – converting the semi-natural socio-ecological miombo in to more human dominated production oriented landscape – it results in more species *losers than winners*, reduces diversity and alters the intactness of communities of the two taxonomic groups we investigated. However, although trees and mammals both consequently declined in species richness as woodlands became more fragmented, they showed dissimilar patterns. Tree communities lost species linearly with each unit increase in fragmentation, irrespective of the quantity of woodland cover. Mammals, on the other hand, showed a non-linear response. The species richness of mammal communities increased at the intermediate stages of fragmentation and started to decline only after fragmentation reached beyond ~60% and the remnant woodland cover reduced below ~27%. Beta diversity responses also varied between the two groups. Although tree communities underwent a linear decline in species richness, they maintained diversity at the landscape scale through increases in beta diversity. Tree communities showed increase in turnover and decrease in the nestedness component of beta diversity in

more fragmented landscapes. This means, in terms of species compositions, they drifted away from the tree communities in less fragmented and high woodland cover landscapes. In contrast, mammal communities not only lost species richness but also beta diversity. They became increasingly homogenous mainly due to decrease in the quantity of woodland cover in the fragmented landscape. So, agricultural expansion-led fragmentation and woodland cover loss is associated with reduction in species richness across both taxonomic groups – trees and mammals. However, mammals have non-linear response to fragmentation and follow the threshold hypothesis (fragmentation affects after habitat quantities declines beyond a threshold; Andrén 1994), whereas tree communities lose species with every unit increase in fragmentation and do not undergo a sudden regime shift. Fragmentation further is associated directly with drifts in composition of tree communities and indirectly, through habitat loss, with taxonomic convergence of mammal communities. Therefore, in short, agricultural expansion in the miombo woodlands causes subtractive heterogenization of trees and subtractive homogenisation of mammals.

RQ3. How does human and elephant disturbance modify habitat structure and alter bird communities in the mopane woodlands?

In the third data chapter (chapter 4) of this thesis, I investigated if humans and elephants have dissimilar effects on the structure of mopane woodlands and its biodiversity. I found that there are three distinct structural forms of mopane woodlands in Zambia, and elephants and humans are associated with different structural forms. Further, the results show that elephant and human disturbances affect different structural attributes in dissimilar ways. Although, both were associated with reductions in stand density, human disturbance was related to decline in biomass and increase in number of small stems (<10 cm DBH), whereas, elephant disturbance showed no effect on biomass but increase in the size of stems. Elephant affected areas thus potentially maintain biomass through few big trees

which escape the elephant impact threshold (>4 m; Smallie & O'Connor 2000). Furthermore, both the disturbances – humans and elephants, were associated with reduction in species richness of bird communities. However they had dissimilar effects on species composition, functional diversity and functional composition. Elephant disturbance did not affect functional diversity, but was associated with reduction in the species and functional beta diversity, meaning, that bird communities in elephant disturbed areas did not undergo functional convergence, but still became taxonomically and functionally more homogenous at the landscape scale. Human disturbance, on the other hand, did not affect species beta diversity, but was associated with reduction in functional diversity and increase in the nestedness component of functional beta diversity, indicating that bird communities in human disturbed areas converge in functional space and become functional subsets of communities of less human disturbed areas. To answer the above research question, human and elephant disturbances are associated with different habitat structures and affect biodiversity differently. Although, both disturbances are associated with declines in species richness, human disturbance is associated with functional convergence without taxonomic homogenisation, and elephant disturbance is related to taxonomic and functional homogenisation without the loss of functional diversity. In short, human disturbance may cause reductions in species richness and functional diversity, while elephant disturbance may result in reductions in species richness and beta level species and functional diversity without any change in alpha functional diversity.

Thesis conclusions

Below I discuss the above inter-related conclusions (C1-C4) I draw from answering these questions, and compare these results with other related studies, and explain their implications in more detail.

C1. Land use activities in miombo region create more species losers than winners

In RQ1 & RQ2, I showed that the **average population size of trees and mammals trend downwards** in response to land use (charcoal production and agriculture expansion). Occurrence of **majority of species reduced** in areas with high land use pressures. McKinney & Lockwood (1999) compiled evidence suggesting that as majority of species are lost from ecological assemblages (species losers), they are replaced by few widespread exotic and resilient species. Tabarelli et al. (2012) reaffirmed this winner-loser replacement phenomena in context to the native biotas. They demonstrated replacement of old growth tree species by fast growing pioneer species. In this study, tree assemblages showed increase in abundance of few species and reduction of many, in response to both charcoal production and agriculture expansion. Thus my results support the **few winners-many losers replacement (WLR) paradigm** (McKinney *et al.*, 1999; Tabarelli *et al.*, 2012) in the miombo context.

In context to charcoal production, the loser tree species (44 %) consisted of the locally common as well as rare, charcoal, timber and firewood important, old-growth tree species. The few winner species (14 %) comprised of locally widespread but less desired shrubby forms of *Colophospermum mopane*, and other disturbance tolerant - secondary growth species such as *Acacia nilotica kraussiana, Acacia burkei, Boscia spp* and *Diospyros mespiliformis* (PROTA, 2013); mainly the tree species left behind by the charcoal industry. **WLR in response to charcoal production therefore is essentially few locally common *winners* replacing many *species losers* (common**

winner-loser replacement, CW-LR). In the agriculture expansion frontier too, tree communities underwent WLR. However, in response to agriculture-led fragmentation and habitat loss, the many (25%) old growth and key miombo species (*Brachystegia boehmii* and *Brachystegia bussei*) were replaced by few (3.5%) rapidly re-growing and relatively infrequent species such as *Piliostigma thonningi* and *Strychnos spinosa*. In other words, **in response to agriculture expansion, non-widespread and locally infrequent *species winners* replaced many *species losers* (infrequent winner-loser replacement, IW-LR)**. The CW-LR was associated with biotic homogenisation, while IW-LR was correlated with biotic heterogenization in tree communities. For mammals, most species declined (many species losers) and none showed increase (no winners). In charcoal production areas, mammal species losses were correlated with biotic heterogenization, whereas in agriculture land use they were associated with homogenisation. In case of charcoal production, random species losses leaving behind widespread as well as infrequent mammal species could explain their biotic heterogenization. In contrast, loss of sensitive infrequent species and persistence of few widespread resilient species may be a possible explanation for the biotic homogenisation of mammals in response to agriculture expansion. However, these are just speculations as only five mammals in this thesis reached statistical significance (95% CI). More robust multi-season studies are therefore needed to understand population dynamics of mammals more thoroughly.

Although majority of assemblages we investigated showed WLR or just *species losers*, not all of them experienced homogenisation as is widely assumed in the WLR discourses. I propose here that the key word in the WLR framework is "widespread". McKinney & Lockwood (1999) emphasized that biotic homogenization is promoted by replacement of many species by few "widespread" species. In this thesis, I highlight that **substitution by widespread winner species i.e. CW-LR is related to biotic homogenisation, while substitution by rare-infrequent species IW-LR results in biotic heterogenization**.

C2. Land use and disturbance pressures in miombo region reduce species richness

Combining the results of RQ1, RQ2 & RQ3, I confirm that land use (charcoal production and agriculture) and disturbance pressures (human and elephant disturbance) in the miombo and mopane woodlands **reduce species richness at local scales**. I also underline that **species richness trends (loss or gain) patterns (linear or non-linear) are not uniform across taxonomic groups**.

My observation about reduction in species richness corroborates the findings of several global syntheses: land use-biodiversity (Murphy *et al.*, 2014; Newbold *et al.*, 2015), selective logging-biodiversity (Gibson *et al.*, 2011; Clark *et al.*, 2012), and the recent African grassy biome specific study (Newbold *et al.*, 2017). At the same time, it contradicts the syntheses based on temporal comparisons (Vellend *et al.*, 2013; Dornelas *et al.*, 2014).

In this thesis, the average reduction in species richness across all studies was 14.5 % (95 % CI: 2.2-26%). Excluding ground beetles, it came to 18.6% (95 % CI: 7.5-29.7%). In comparison to other studies (Figure 2), this estimate is above the global average of 13.6% suggested by Newbold et al. (2015), closer to the global average of 18.3% observed by Murphy & Romanuk (2014), and lower than the African average - 21.6% described recently by Newbold et al. (2017) and the Tropical average - 25.6% by Murphy & Romanuk (2014). Murphy & Romanuk (2014) and Newbold et al. (2017) point out that tropical biomes and African savanna ecosystem specifically can be more sensitive to biodiversity loss compared to the other biomes possibly because of the land use pressures and their high biodiversity. Although, the estimates of this study are not significantly different (95 % confidence intervals overlap) from those of global estimates, our results also point out towards biodiversity loss in tropics to be of higher magnitude than the other biomes, albeit with large uncertainties.

Furthermore, comparing the changes in species richness observed in this thesis with limits suggested by Hooper et al. (2012), I emphasise that the average species richness losses observed in all the RQs combined (mammals=19.7%, trees=17.5%, Birds=18.6 %) have not exceeded the intermediate threshold (21%). Hooper et al. (2012) compiled evidence suggesting that beyond this threshold, species losses substantially impair the biodiversity driven ecosystem functions and services. They also indicated another higher level limit, 41% species loss, after which ecosystems undergo an extreme shift with consequences equalling nutrient pollution, ozone acidification and CO_2 elevation. Although the **average species richness loss observed in this thesis is below these thresholds**, in the highly affected areas (charcoal land use intensity >3, fragmentation (Land division index, LDI) >75%, human and elephant disturbance>50%), all communities (except those of ground beetles) did surpass the intermediate level (Figure 2). In addition, mammals exceeded even the high level threshold (41%) in the worst affected areas (e.g. charcoal land use intensity 6 and fragmentation (LDI) >85%). Hence, **at their highest intensities, charcoal production and agricultural expansion can reduce species richness with possible consequences** on ecosystem services and goods and well-being of people.

To mitigate the loss of species, future land use management must take in to account the thresholds of land use and tipping points of species richness (Lindenmayer *et al.*, 2005). Land use intensity should be maintained below these thresholds to conserve biodiversity (Lindenmayer *et al.*, 2005). For the land use activities I investigated, an approximate estimate for their thresholds can be: intensity class 3 for charcoal production, 75% fragmentation, and 50% human and elephant disturbance. Identifying thresholds for land use activities is however more complex and is dependent upon measures and definition of land use intensity (Lindenmayer *et al.*, 2005; Erb *et al.*, 2013) and the biodiversity measured (Mönkkönen *et al.*, 1999; Lindenmayer *et al.*, 2005). Therefore, more studies are needed to specifically identify land use intensity thresholds and biodiversity tipping points.

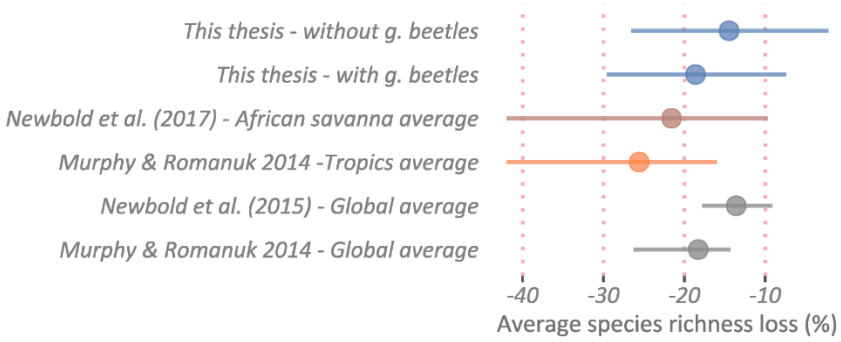


Figure 2: The estimated average species loss in this thesis is more (but not significantly different) than the global averages estimated by the two recent global syntheses. Also it is closer to the tropic and African averages, together suggesting that biodiversity loss in the African savanna woodlands may be more severe than other biomes. Also note: Murphy & Romanuk (2014) mentioned only average estimates in their paper, I extracted CI using GetData Graph Digitizer software (S. Fedorov, Russia), the averages based on CI limits in their figures slightly deviate from the average estimates mentioned in their publication. Here, I used the mean estimates in their text and the CI from the figures.

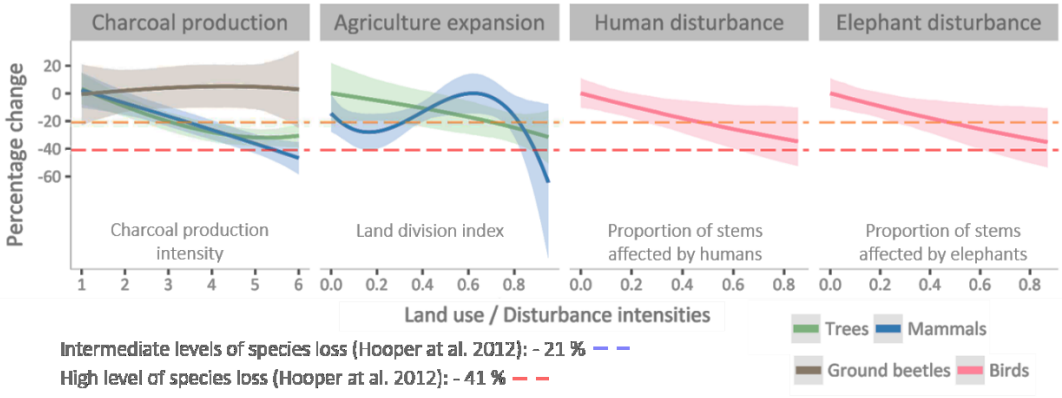


Figure 3: Species loss estimates here show that all taxonomic groups, except ground beetles, declined in richness. Their trends compared with ecosystem thresholds identified by Hooper et al. (2012) highlight that in the high land use intensities communities undergo intermediate to high level species loss. Such losses substantially impair biodiversity-led ecosystem services.

Here, I also highlight that the **species richness trends differ between taxonomic groups**. In RQ1, I found that ground beetle communities did not reduce in species richness, while those of trees and mammals did (RQ1). Heterogeneity in response between taxonomic groups have been observed in other studies (Berry *et al.*, 2010; Burivalova *et al.*, 2014). However, Newbold et al. (2015) revealed absence of any significant taxonomic group effect. Also, my observation partly differs from that of Burivalova et al. (2014) who, while demonstrating heterogeneity between taxonomic groups, also indicated reduction in species richness of invertebrates in response to

logging intensity. However, Burivalova et al. (2014) included butterflies, dung beetles, and ants, whereas I studied only ground dwelling beetles in the invertebrate group. Nevertheless, the inference that the diversity and composition of ground beetles remain unchanged (or increased) in response to selective logging is supported by the global ground beetle-habitat modification synthesis (Nichols *et al.*, 2007) among other studies (Davis, 2000; Hayes *et al.*, 2009; Berry *et al.*, 2010).

Further, even though the trends, the direction of change, are similar, I found that **species richness patterns (linear - nonlinear) are however different between taxonomic groups**. This has important implication for the threshold concept I discussed above. This finding, supports the claims made by Mönkkönen & Reunanen (1999) and Lindenmayer & Luck (2005). It primarily suggests that a one threshold may not represent all taxonomic groups because different patterns will involve different thresholds. I explain this below.

Biodiversity is not a linear function of land scape (Mönkkönen *et al.*, 1999). In RQ2, I showed that **trees undergo a gradual decline in species richness in response to fragmentation, while mammals experience a regime shift** beyond a fragmentation (75 %) and habitat quantity threshold (26.5%). This refutes the widespread habitat threshold notion which claims that fragmentation affects only after the quantity of habitats go below 30 %. Findings in this thesis show that the critical threshold theory (Andrén, 1994; Hill *et al.*, 1999; With *et al.*, 2011) is valid for mammals but not for trees, thus underscoring the differences between taxonomic groups.

In conclusion, species richness primarily reduces in response to land use pressures. However, there are caveats - taxonomic (taxonomic group) heterogeneity should be taken in to consideration. Further studies are required to identify land use thresholds and biodiversity tipping points for mitigation of future species losses.

C3. Different land use activities impose dissimilar ecological filters on different taxonomic groups

In this thesis I show that, inspite of losing species, not all communities underwent a total biodiversity decline. Mammal communities in high intensity charcoal production and tree communities in response to fragmentation due to agricultural expansion increased in beta diversity. In addition, bird communities in human disturbed areas maintained beta diversity of species and functional groups, they did not undergo biotic homogenization - species or functional. Bringing back the WLR paradigm and the species richness loss discussion here, I restate that WLR and **reduction in species richness do not always lead to biotic homogenization**. Some communities maintain biodiversity at the meta-community scale through increase in dissimilarity between communities – the spatial beta diversity. Here, meta-community refers to a spatial set of communities which are linked by dispersal and source-sink dynamics. Which essentially implies that populations and diversities can be maintained at a landscape scale through beta diversity (Tscharntke *et al.*, 2012). With time, the local communities may recover the lost diversity through immigration or dispersal of species from sources (where growth rates are higher) to sinks (where population has diminished). This highlights the resilience of spatially heterogeneous communities and importance of beta diversity as a spatial insurance.

Beta diversity patterns can arise due to inherent species traits (Ackerly *et al.*, 2007; Kraft *et al.*, 2008; Siefert *et al.*, 2013; Aberer *et al.*, 2014) or as consequences of habitat or environment filters (Kessler *et al.*, 2009; De Cáceres *et al.*, 2012; Myers *et al.*, 2013). In my studies here, I found dissimilar patterns of beta diversity between taxonomic groups and land use activities. I suspect that these heterogeneous patterns are results of dissimilar filtering processes imposed by different land use practices. Below I provide plausible explanations and implications of this pattern.

In RQ1, I showed that charcoal production selectively removed many tree species resulting in CW-LR and, as result, biotic homogenisation of trees. Similar

observations were made by Kalaba et al. (2013) and Ndegwa et al. (2016). The charcoal production in the mopane woodlands did not result in loss of vegetation cover as the dominant species in the region, *C. mopane*, was retained, albeit as a secondary growth. However, charcoal production is known to decrease the quality of habitats by depleting woody biomass (Chidumayo, 1993; Ndegwa *et al.*, 2016; Woollen *et al.*, 2016). This may have affected mammal communities indirectly by random habitat filtering through competitive exclusions (Segre *et al.*, 2014; Püttker *et al.*, 2015) leading to random local extinctions. As a consequence, mammal communities became increasingly dissimilar in species composition leading to biotic heterogenization i.e. increases in beta diversity. Similar observations have been made, although in an altogether different ecosystem and land use, by Woodcock & Yu (2015). Also, in RQ3, bird communities maintained beta diversity while they lost species richness. Potentially, bird communities in response to human-habitat disturbance were subjected to similar selection processes as that of mammals in response to selective logging for charcoal production.

In agricultural land use (RQ2), fragmentation imposed similar random filtering processes on trees, but not on mammals. When miombo woodlands are cleared for agriculture expansion (Ryan *et al.*, 2012, 2014), removal of trees is random and not selective like in charcoal production. This causes random loss of many tree species, which subsequently are replaced by few infrequent rapid-growing secondary vegetation species (IW-LR). Hence, tree communities in secondary growth become compositionally distinct. In other words, undergo ecological drift, increase in beta diversity or experience biotic heterogeneity. Mammals in these fragmented landscapes undergo deterministic reduction leading to a strong biotic homogenisation i.e. reduction in beta diversity. This is mainly because, as the woodland habitat in the woodland-agriculture mosaic shrinks and becomes fragmented, disturbance sensitive species with preference for woodland habitats decline, and are replaced by disturbance tolerant species which survive in the non-woodland matrix. This finding, which also matches observations by Püttker et al.

(2015), contests the widespread notion that communities in fragmented landscapes undergo ecological drift. I reiterate that **different taxonomic groups respond in dissimilar ways to different land use activities**. In response to fragmentation in the miombo woodlands, trees indeed undergo ecological drift, but mammals do not.

Many studies show that communities in secondary vegetation are compositionally distinct and have lower species richness than those in primary vegetation (Martin *et al.*, 2004; Gibson *et al.*, 2011; Newbold *et al.*, 2015). Also, evidence suggests that this difference between primary and secondary vegetation reduces as diversity recovers with the maturity of secondary vegetation (Gemerden *et al.*, 2003; Dunn, 2004; Martin *et al.*, 2004; Bonnell *et al.*, 2011; McNicol *et al.*, 2015). However, there are also number of studies demonstrating no recovery of alpha or beta diversity (e.g. Williams et al. 2008; Strømgaard 1986). This inconsistency is potentially due to uncertainty in time required for recovery (Williams *et al.*, 2008), which also depends on the intensity of land use and other human disturbances (Chazdon, 2003; Dent *et al.*, 2009) in addition to dispersability - availability of the original species (Gorchov *et al.*, 1993; Vleut *et al.*, 2015). I emphasise here that **recovery may also depend upon the spatial beta diversity state of communities.** Communities which have experienced biotic heterogenization are more likely to recover as species needed for recovery are maintained in the meta-community species pool (Tscharntke *et al.*, 2012). Thus, mammals in the charcoal production landscapes, birds in human disturbed habitats, and tree communities in the fragmented agricultural landscapes have possibility of recovery as they maintain spatial beta diversities.

C4. Effects of humans and elephants on habitat structure and functional diversity are not interchangeable

Tree removal by humans and elephants influences the structure of the woodlands in the miombo region (Guldemond *et al.*, 2008). Superficially these two disturbances appear similar and their effects interchangeable. However, my observations in RQ3 underline the nuanced differences between the effects of elephants and humans on

the structural attributes of mopane woodlands, and species and functional diversity of birds in it. I found, that reduction in stem density was more severe in case of elephant disturbance. In other words, **magnitude of tree removal by elephants was higher than that of humans.** However, despite the higher impact on stem density, elephant disturbance did not significantly reduce the plot level mean woody cover (i.e. basal area). This was mainly because the remaining trees in the elephant impacted plots were of larger size classes (>30 cm DBH) counterbalancing the woody cover loss due to removed trees. This means that the **woody biomass in more elephant dominated landscapes is stored in the few large trees which escaped the elephant impact** threshold and were not any more vulnerable to the elephant browsing. This finding endorses the existence of "browse trap" (Staver *et al.*, 2014). By contrast, intensity of human disturbance was associated with significant reduction in mean woody cover and increase in density of small stems (< 10 cm DBH). This observation partially matches with my findings in RQ1 of this thesis, where selective logging for charcoal production was associated with decrease in standing woody cover and increase in number stems of shrub-form *C. mopane*, albeit not reaching statistical significance at 95% CI. However, similar observations (a decline in number of large size stems and persistence of low quality secondary growth *C. mopane*) have been made by others (Backéus *et al.*, 2006; Fontodji *et al.*, 2011; Woollen *et al.*, 2016; Kiruki *et al.*, 2017). I speculate here, that in contrast to the elephant impact, there is no apparent escape to the "human trap." In human dominated areas, large mopane stems are selectively logged for charcoal production, a dominant land use activity in the region, leaving behind the undesired smaller or coppicing low quality stems which can be used for firewood or are left for cattle to browse. In this study, I further identified three structurally distinct forms of mopane woodlands in Zambia and showed they are related to different intensities of human and elephant impact. Hence, demonstrating that **disturbance by humans and elephants can lead to different structural forms of the mopane woodlands**. Thus, with the increasing human dominance, savanna woodlands are more likely to become low woody biomass systems. Using bird

communities to indicate biodiversity, I demonstrated the dissimilar effects of humans and elephants on species and functional diversity. I showed that human disturbance is associated with reduction in species richness and loss of functional diversity in human dominated areas, and even through elephants were also associated with reduction in species richness, they had no effect on functional diversity. The main reason behind this could be that bird communities underwent competitive exclusions and lost the commonly occurring functionally unique species – the insectivore-feeders (*Batis molitor* and *Prinia subflava*), while elephant affected areas retained functionally unique species such as *Agapornis lilianae* and lost the redundant and locally infrequent non-woodland species such as *Quelea quelea*. The common-common replacement in case of **human-disturbance lead to subtraction of species and functional diversity** in communities without homogenisation. The rare-common replacement in response to **elephant-disturbance led to subtraction in species diversity and biotic homogenisation, but did not affect functional diversity** of communities. This is the key difference between the effects of elephant and human disturbance. To summarise, my study provides evidence that humans and elephants modify habitat and biodiversity in dissimilar ways. Based on this single season spatial comparison of habitat attributes and bird communities across mopane woodlands in Zambia, I state that **if loss of woody biomass and functional diversity is a matter of concern, human disturbance is "bad", while, elephant disturbance is not**. Comparing the difference in habitat and biodiversity impacts of these two disturbances and disentangling the relative contributions of climatic and edaphic factors still needs more attention.

Limitations of this thesis

One limitation of all the research questions I explored as part of this thesis is that their results depend on many assumptions. I used space-for-time substitution to answer all research questions in this thesis. My conclusions about the effect of land use activity or disturbance, therefore, assumes that the observed patterns are result of the land use or disturbance histories of the sites (or plots) I compared. However, this assumption holds a considerable validity because the study areas we investigated we similar in land cover. Sites in RQ1 and RQ2, were 100 km of each other and for RQ3 I took in to account variability due to distance from river, lakes, cities and protected areas. However, I did not consider the land use history of the sites. The protected areas, especially, may have contrasting history even though they are ecologically similar. Nonetheless, I agree that temporal comparison is a better and more ideal choice. However, the space-for-time substitutions have been one of the commonly used methods to studying ecological patterns and number of spatial comparisons have found results identical to my findings. My observations provide an estimate of the trends and possible patterns which indicate towards the need to carry more research, which could include long-term temporal and multiple spatial assessments.

All studies in this thesis compare land use activities which entail removal of woody cover. However regrowth of trees through coppicing is common in southern Africa. We did not explicitly consider the effect of regrowth thereby overlooking the resilience ability of these ecosystems. The biodiversity surveys on which our estimations of biodiversity change are based were single season surveys performed in the early dry season (May-August). The invertebrate populations could be lowest during these times. Thus we may have underestimate the sensitivity of insect groups to land use pressures (selective logging for charcoal production). Response of their taxonomic groups – mammals and birds, may be seasonal too, and with our single season study we most possibly overlooked the seasonal variation which undermines our ability to generalize our findings. We also did not specifically

distinguish between effects of hunting and grazing which could also bias our results. However, since the plots we compared had similar conditions, the trends observed in this study should be robust.

The way forward

In this thesis, I frequently point out that despite losing species and experiencing reductions in species richness, not all taxonomic groups undergo spatial biotic homogenisation. Some show increase or no change in beta diversity, hence maintaining biodiversity at the meta-community scale. Based on this, I claimed that the spatial beta diversity improves resilience and provides spatial insurance through dispersal-led source-sink dynamics. I further speculated that abandoned disturbed areas may recover richness and composition of taxonomic groups that have maintained the spatial beta diversity. Although number of studies have investigated the processes of recovery in the abandoned fields and degraded woodlands, none have systematically studied the role of beta diversity, the meta-community species pool. Understanding the role of beta diversity patterns in recovery and restoration of woodland ecology is the thus a promising avenue of research in the context of miombo.

The biodiversity in the savanna woodlands is dynamic and adapted to the disturbances. A single season study like mine points out toward possible patterns, but does not capture the true nature of ecological communities in these woodlands. A way forward could be a long term monitoring of landscapes representing an intensity gradient of different land use activities and disturbances (charcoal production, small-scale farming and habitat disturbance). This will improve our understanding of similarities and differences between the effects of major land use activities and disturbances and help predict the patterns of biodiversity change and its consequences.

Biodiversity monitoring is challenging and resource intensive. Developing tools and methods for rapid biodiversity assessments is an urgent need. Identifying new methods for automated biodiversity sampling using acoustic recorders, satellites and cameras is another emerging area work that can help understand biodiversity dynamics of the savanna woodlands better.

The Miombo–Mopane woodlands are relatively more intact ecosystems compared to the other tropical biomes (Mittermeier et al., 2003; Newbold et al., 2017). However, with increasing rates of disturbance (deforestation and degradation) due to the growing demands of people for food, timber and fuelwood (Mittermeier et al., 2003; Kutsch et al., 2011; Schneibel et al., 2016), the potential and intensity of future biodiversity loss in these ecosystems are likely to be higher (Mittermeier et al., 2003; Newbold et al., 2015). For conservation of biodiversity in this region, the understanding of the patterns of biodiversity change in response to the disturbances is important. This understanding can be used to inform the policies for sustainable land management and biodiversity conservation in the area.

Our studies here highlight that the major land use activities – selective logging for charcoal production and agriculture expansion and habitat disturbances result in loss of species at local scales. However, these studies also point out that loss of alpha diversity does not always entail reductions in beta diversity, and different taxonomic groups respond to land use mediated disturbances in different ways. To minimize the biodiversity trade-offs (loss of alpha and/or beta diversity) and for the conservation of biodiversity, the planning and management of land use activities must be done taking in to account multiple spatial scales – local (community) and landscape (meta-community).

The selective logging for charcoal production resulted in a loss of beta-diversity of tree species and no changes in that of mammals. At the landscape scale, beta diversity can restore alpha diversity by source-sink dynamics (Tscharntke et al., 2012). Thus, in case of charcoal production, biodiversity conservation must focus on

tree communities. Charcoal production switches from selective logging to 'take anything' regime as charcoal production intensifies - demand for charcoal increases and supply of preferred species and their stem sizes reduces (Philomena Kumapley et al., 2016; Woollen et al., 2016). To reduce the impact of charcoal production on beta-diversity of trees, increased intensification should be avoided and charcoal production must remain highly selective in the species and size of trees extracted. Reduced intensification will result in small reductions in alpha diversity while beta diversity is more likely to be maintained as locally infrequent species winners replace the few dominant species losers. In order to avoid intensification, the charcoal frontier should continue to expand to new areas leaving behind the exploited areas for regeneration and recovery of woodlands (Woollen et al., 2016).

Agriculture expansion, unlike charcoal production, causes reduction in beta diversity of mammals and increase in that of trees. Tree communities, as shown by McNicol et al., (2015), may recover through source-sink dynamics once the fields are abandoned. Mammal communities, however, are predisposed to local extinctions due to the combined effects of fragmentation and habitat loss. To manage the effects of agriculture expansion, the increases in degree of fragmentation and decreases in woodland quantity must be avoided. In this study, and in the wider literature of fragmentation and habitat quantity (Andrén, 1994; Fahrig, 2002; Hanski, 2015), the minimum habitat of 25-30% and the maximum fragmentation of ~75% is recommended for maintenance of biodiversity. Fragmentation and woodland quantity in the agriculture-dominated miombo landscape should be maintained within these thresholds.

In the studies here, we focused on multiple species of multiple taxonomic groups. Since none of the species negatively affected by any of the land use activities were of national or global conservation significance (IUCN, 2010), a species-specific conservation activities are not required. Policy interventions at the landscape level, instead, can benefit a large number of species simultaneously. These policies should

focus on maintaining charcoal production at low intensities and reducing the level of land clearing and fragmentation.

With increasing densities and demands of people, land use is more likely to intensify and expand and continue to be a major threat to biodiversity (Johnson et al., 2017). Finding a balance between land use intensification and reductions in biodiversity decline is inevitable and a key challenge (Johnson et al., 2017). To meet this challenge, substantial increases in conservation efforts - policies and practices - in addition to, sustainable management of land leading to increases in yield, reduction in fragmentation and demand of land, and restoration of exploited habitats is required (Tilman et al., 2017). These actions, however, implicate economic costs as they entail underutilization and/or sparing of local resources. Thus, they require incentive-based mechanisms to offset economic costs and facilitate protection and restoration of biodiversity (Dewees et al., 2010). Incentive-based policy instruments are possibly one of the most effective ways of mitigating the biodiversity impacts of land use intensification (de Vries et al., 2016).

The incentive-based policy instruments stem from the concept that biodiversity is a public good and its conservation is a service (de Vries et al., 2016). These goods and services are provided or secured by the land managers who are compensated through public funds (domestic or international funds) or private sector (direct payments or through other market-based mechanisms) for the additional costs they incur for biodiversity conservation and sustainable land use management (Ansell et al., 2016). Payments for ecosystem services (PES) is a highly promising and widely applied policy tool to raise new funding for conservation and create 'win-win' scenarios (de Vries et al., 2016).

Convention on Biological Diversity (COP10; CBD, 2010) included PES as a key funding source for biodiversity conservation (Hein et al., 2013). PES funding can be grouped in to non-market and market (Hein et al., 2013). While market funding is not yet widely applied in the developing countries, nonmarket funding is relatively

the most common source biodiversity aid (Hein et al., 2013). Nonmarket funds comprises the domestic budget allocations form the governments, biodiversity-related multilateral and bilateral aids, and grants from private foundations and charitable trusts and conservation NGOs (Hein et al., 2013).

Reduced Emissions from Degradation and Deforestation (REDD) mechanism is one of most commonly cited example of market-oriented PES funding (Wendland et al., 2010). It was initiated in 2007 by the parties to the United Nations Framework Convention on Climate Change (UNFCCC) with an aim to financially compensate developing countries for protecting their forests in return for carbon sequestration and storage service (Hein et al., 2013). Since carbon stocks are also correlated with the number of threatened mammal, amphibian, and bird species occurring in an ecosystem, REDD can also be an important contributor to funds for biodiversity conservation (Hein et al., 2013).

The Aichi targets (CBD, 2010) restoration of 15% of degraded lands and Bonn challenge (Bonn Challenge, 2011) of restoring 350 million hectares by 2030, largely funded by governments and international bodies, also present a unique opportunity for biodiversity conservation funding. Biodiversity conservation can piggyback these targets and complement their outcomes as the increase in forest cover is more likely to also result in positive effects on biodiversity.

In Africa, PES is at a nascent stage, but will become as one of key drivers of biodiversity conservation as it is gradually expanding into the tropics(de Vries et al., 2016). In the contexts of the finding of this thesis, selective logging for charcoal production which leads to loss of woody biomass without significant changes in the type of land cover will benefit from incentives for maintaining low-intensity charcoal production and restoration of highly exploited areas. In case of agricultural expansion, compensating for land sparing and reduced land clearing through market (REDD and development of alternative livelihood tourism) or non-market (biodiversity aids) funds will reduce the biodiversity impacts of agriculture.

Wrapping up

In this thesis, I explored the patterns of biodiversity response to major land use activities and disturbances using multiple taxonomic groups and at multiple levels: species and community. I concluded that **land use activities in the miombo region create more *species losers than winners*** as they reduce population size of majority of species. I also confirmed that **land use and disturbance pressures in the miombo and mopane woodlands reduce species richness**. I further highlighted that the **species richness trends differ between taxonomic groups** as I found that ground beetle communities did not reduce in species richness, while those of trees and mammals did. Also, I revealed that trees undergo a gradual decline in species richness in response to fragmentation, while mammals experience a regime shift beyond the fragmentation and habitat quantity threshold. I showed that **species losses do not always mean biotic homogenisation**. The variability in beta diversity patterns point out that **different land use activities impose dissimilar ecological filters** on different taxonomic groups. Further, I showed, although humans and elephants seem to be similar habitat disturbance agents, both removing trees, their **effects on the overall habitat structure are not interchangeable**. They lead to different structural forms of mopane woodlands by affecting structural attributes in dissimilar ways. In addition, I also showed that humans and elephants affect the functional diversity and composition of bird communities in differently. Thus concluding that the apparently **similar disturbances, having identical effects on species diversity, may have different functional consequences.**

Findings of this thesis may contribute to the broader understanding of how we should view biodiversity change. T**he loss of species richness may not be the end of the world**, as diversity is maintained at the meta-community state if there is an increase in beta diversity. Furthermore, different land use activities have different ways of organising the species and functional diversity of communities. This becomes even more complicated as the patterns of community organisation also vary between taxonomic groups. The future projections of biodiversity change, and

the local conservation and land use management policies therefore must take in to account these heterogeneities (taxonomic group, land use, and beta diversity). More importantly, **the context matters.**

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